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Natural variation in merchantable stem biomass among clones of trembling aspen

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Natural variation in merchantable stem biomass among clones of trembling aspen submitted by GORDON A. LEHN in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in FOREST SCIENCE.

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DEDICATION

To my wife Meryle

for the support and encouragement she provided

ABSTRACT

In terms of coppice reproduction, genetic variability, and fast growth, trembling aspen occupies a unique position in our forests. These factors need to be given serious consideration in developing aspen management practices.

This study examined various traits of aspen which relate to currently useable biomass production, and analyzed them in terms of probable management strategies. The stocking and size of aspen clones was examined. Inter- and intra-clonal variation in biomass production was studied on two different sites on an areal and individual tree basis. Finally, the relative effects of site and genetic control over production were examined.

Two different sets of clones were studied: one set on a good quality site (near Blue Ridge, Alberta) and the other on a site considered to be of poor quality for aspen growth (near Nordegg, Alberta).

Clonal area varied up to 10 fold in each of the sites examined. Clone size is probably related more to stand history than to environmental or site conditions.

There were significant differences among clones in stem biomass in each of the two study areas, as well as a significant difference in the average biomass per tree between the two sites. Due to less rigorous natural selection against poorly adapted clones, the Blue Ridge site had greater variation in actual biomass.

There was both a greater range and a higher average stocking level at Nordegg. The harshness of the Nordegg site caused that stand to be at an earlier developmental stage. Occasionally a clone combined the desireable characteristics of high stocking levels and a large average tree size.

Biomass per hectare significantly differed among clones on both sites. The difference in average biomass per hectare between the two sites, while significant, was less than the difference in tree biomass between the sites, because of the effect of stocking levels. The better site was 8 times more productive than the poor site in average stem biomass, but 6.5 times more productive in overall biomass per hectare. A 6.5 fold increase in biomass per hectare on one site over another indicates that site selection is critical to aspen management.

Broad sense heritability estimates for bole biomass were moderate. Approximately one-third of the variation in biomass of trees growing on each site was due to clonal or genetic control.

The results of this study indicate considerable possible gains from clonal selection. At the Blue Ridge site, gains could be as high as 43.9 kilograms per stem, of the clones measured. Selection programs should be concentrated on medium and good sites where they will obtain the best results.

Aspen exhibits a phenomenal amount of variability among clones in almost every aspect. It is, therefore, important

that the clone be the basic sampling unit in any type of forest inventory or site productivity work. It should be considered in all decisions pertaining to aspen management.

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I. INTRODUCTION

Trembling aspen (Populus tremuloides Michx.) is the most widely distributed tree species in North America (Harlow and Harrar 1969). Its range is shown in Figure 1.

Ten percent of the forest cover in Canada consists of members of the genus Populus; 81 percent of this is trembling aspen. In Alberta, approximately 40 percent of the timber resources are deciduous; 80 percent of these are trembling aspen (Neilson 1974).

For years, aspen has been regarded as a weed species. However, in the United States, aspen is presently being looked upon as a major forest species, one which could potentially supply an important future timber resource (Johnston and Bartos 1977).

Market trends and public awareness over the gradual depletion of our fossil fuels are changing. Forest industry and government are gradually starting to investigate the possibility of utilizing this vast poplar resource for both timber and as a source of biomass for the production of methane, methanol and other chemicals.

Aspen grows under a wide range of site conditions and shows considerable variation in growth on different sites (Einspahr and Benson 1967, Maini 1968). On poor sites aspen may never attain merchantable size (Maini 1968), whereas on medium and better quality sites aspen has been observed to grow more rapidly than any of our other native tree species

Figure 1. The range of trembling aspen (Populus tremuloides Michx.) (after Fowells 1965).

(Jones and Markstron 1973).

Throughout its range, aspen stands are generally comprised of a mosaic of clones (Barnes 1966 and 1969, Basham 1958, Copony and Barnes 1974, Fralish 1972, Jones and Markstron 1973, Kemperman and Barnes 1976, Steneker and Wall 1970, Steneker 1972, Wall 1971, and Zahner and Crawford 1965). The single stem is the unit of development of most North American tree species, but the typical unit of growth and development in aspen is the clone. Each clone is a group of genetically identical individuals (ramets) arising vegetatively (through suckering) from a single parent (ortet). Each ramet within a clone has similar phenotypic, growth, and quality characteristics (Barnes 1969, Blake 1964, Einspaher and Benson 1967, Jones and Trujillio 1975a and 1975b, Steneker 1970 and 1972, and Zahner and Crawford 1965). Zahner and Crawford (1965) and Barnes (1969) documented large differences in growth rates of different aspen clones on a shared site. Graham, Harrison, and Wendell (1963) commented that differences in clonal growth rates could provide foresters with opportunities for genetic selection. If the differences are common and statistically significant it may be wise to manage aspen on a clonal basis, promoting the more superior clones, rather than on a stand basis.

Aspen grows in a broad spectrum of environments and is probably made up of a wide range of adapted genotypes. It is possible, however, that morphological peculiarities may

simply be a response of the species in general to some environmental condition at the site. For any type of species management it is important to be able to know and separate the relative effects of site and genotype on growth.

This is the basis from which the following hypotheses and objectives to be dealt with in this study were derived.

Hypotheses

1. There are no differences in biomass per tree among equal-aged aspen clones on a shared site.
2. There are no differences in biomass per tree between equal-aged aspen stands, averaged over clones, on two dissimilar sites.
3. There are no differences in biomass per hectare among equal-aged aspen clones on a shared site.
4. There are no differences in biomass per hectare between equal-aged aspen stands, averaged over clones, on two dissimilar sites.

Additional Objectives

1. To examine the range of variability of the area occupied by clones within and between two dissimilar sites.
2. To examine the range and variability of clonal stocking levels both within and between two dissimilar sites.
3. To examine the relative importances of genetic and site control on biomass production on two different sites.

II. DESCRIPTION OF STUDY AREAS

It is important to determine whether productivity of clones is determined by site or if it is a species-related phenomenon. By choosing two very different sites, greater confidence can be placed on any observed trends. The two study areas in this project were located in different forest regions; one in a northern boreal, the other in a subalpine region (Rowe 1972). The boreal site was located just north of the town of Blue Ridge, Alberta (lat. 54° 12' N., long. 115° 26' W.); and the subalpine site was west of Nordegg, Alberta (lat. 52° 25' N., long. 116° 34' W.).

The choice of sites was based on three main criteria. The first was that each study area would have relatively unform climate, soils, slope, aspect, and drainage throughout. By minimizing variation within an area it should be easier to examine differences in productivity due to clonal effects. The second criterion was that the stands in both study areas would be approximately the same age. The biomass distribution of a tree varies with size and age (Jones and Markstron 1973). It was hoped that by choosing areas with similar ages the proportion of biomass in the bole would be standardized. The third criterion was that environmental conditions at each study area would be different. By comparing two contrasting areas, both the magnitude of the productivity differences between sites could be examined as well as the effect of site severity on

production between clones.

Fralish and Loucks (1975) summarizing the results of other researchers, described the various factors influencing site quality: soil texture, chemical and nutrient properties, soil moisture, depth to water table, exposure, aspect and slope, fire history, insects and diseases, and climate. It is not feasible, however, to incorporate all of this information into a field assessment of site quality (Heinselman and Zasada 1955). According to Heinselman and Zasada (1955), Steneker (1976), and Stoeckeler (1960), soil texture and drainage are two of the most important factors. Therefore, the information collected for this study consisted of factors which relate most directly to the moisture status of the site.

Table 1 presents some of the major parameters that may affect site quality in each of the two study areas.

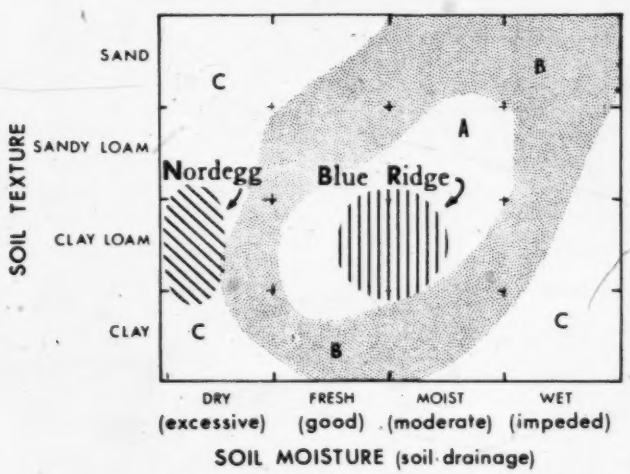
Table 1. Table of major parameters affecting site quality for the two study areas.

Characteristic	Nordegg	Blue Ridge
Soil texture	clay loam	clay loam
Drainage	excessive	well to mod. well
Topography	severly hilled	flat to gently rolling
Aspect	SSE	flat
Slope	30%-50%	0%-5%
Elevation	1550-1580 meters	730 meters
Average age	90 years	80 years

The best soil texture for aspen growth is a loam with moderate permeability (Heinselman and Zasada 1955 and

Steneker 1976). Both study areas had similar clay loam soil textures. However, in terms of soil moisture or drainage conditions, the Blue Ridge area was more favourable to aspen growth. Steneker (1976) presented a site quality matrix of soil texture, moisture, and drainage conditions. This matrix was used to compare site qualities of each of the study areas (Figure 2).

Figure 2. Matrix of soil texture, moisture, and drainage conditions indicating good (A), intermediate (B), and poor (C) aspen sites (adapted from Steneker 1976).



The relative positions of the Nordegg and Blue Ridge study sites are indicated.

According to this classification, Blue Ridge would be considered a good aspen site and Nordegg a poor one.

The southerly aspect of the Nordegg site on a fairly

steep hill compounds the drying effects which result in poor growth. A further complicating factor is the presence of a subangular blocky soil structure 20 cm below the surface which seems to act as a hardpan for water and root penetration. Heinselman and Zasada (1955) pointed out that the combination of dry soils and bedrock at a depth less than 25 cm is one of the poorest situations for aspen growth.

The site characteristics outlined in Table 1 have implications in terms of possible sources of error. Since the two areas have different site qualities, there are some problems in making direct comparisons. For example, poorer sites generally have a greater incidence of decay (Steneker 1976). The logical corollary to this is for stands on poorer sites to show earlier signs of decadence (Heinselman and Zasada 1955). In addition, the proportion of biomass allocated to various tree components varies. Jones and Trujillio (1975a) noted that on harsh sites, a great amount of the biomass production is allocated to the crown. There is a difference of 850 m in elevation between the two sites. Greene (1971) pointed out that this could affect stand longevity; the higher the altitude, the greater the lifespan. Greene (1971) attributed this to lack of disease, fewer fires, and slower diameter growth. This appears to work in opposition to the decadence trend noted by Steneker (1976). Although the soils and moisture status of the Nordegg site result in poor aspen growth, the increase in

elevation may counteract the accelerated spread of decay, thus tending to equalize longevity on the two sites.

The Nordegg site is on a steep slope with a 30 m elevational change within the stand. However, Peterson, Chan, and Cragg (1970) claimed that above-ground biomass among clones should not be influenced by the position on the slope.

III. METHODS AND MATERIALS

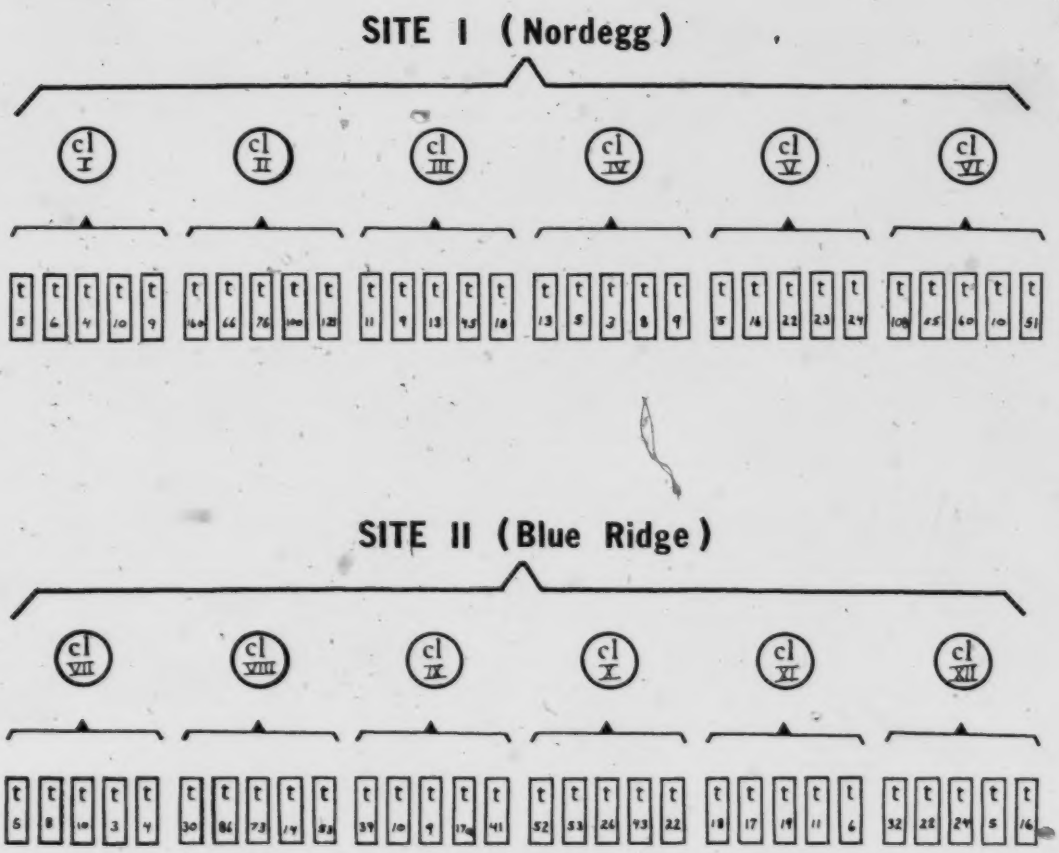
Because various clones react differently to the same site conditions (Zahner and Crawford 1965) many clones should be sampled in order to arrive at a correct estimation of site quality. Also, the larger the sample size the greater the confidence which can be placed on any observed trends among the clones. However, given the logistic restrictions of time, money, labour, and equipment a reduced sample size was used. Following the recommendations of Zahner and Crawford (1965), six clones were sampled at each of the study areas.

The restrictions mentioned above also limited the number of trees sampled in each clone. Five sample trees were randomly chosen to represent each clone (Figure 3).

Barnes (1969) noted considerable phenological diversity among sites and among clones on a given site. Furthermore, he noted that it was the amount and nature of this clonal variation which allowed them to be delineated. Barnes (1969), Jones and Harper (1976), and Steneker (1976), have discussed criteria for distinguishing clones. Flushing time, leaf coloration, time of leaf fall, incidence of decay, bark texture and color, and stem form are some commonly mentioned traits useful in clonal delineation.

The key trait used to delineate clonal boundaries in this study was time of leaf flush. Other characteristics used to help identify clones were: bark texture and color,

Figure 3. Sampling design showing the number of trees sampled per clone and the number of clones sampled on each site.



Note: The clone and tree numbers given in this figure correspond to the actual clones and trees as illustrated in the clonal maps (Appendix I) and the raw field data (Appendix II).

stem form, branching habit, and incidence of galls and cankers. Clones used in this study had boundaries which could be definitely identified. In addition, clones which showed obvious differences in area, stocking, tree size, or other characteristics were selected. This was done to include the range of clonal characteristics which were present in the area.

Trees of the same clone were flagged and numbered. A grid was then layed out through the clone using rows of string placed a few meters apart. This aided in drawing field maps for each clone. The nearest surrounding trees outside of the clone were also mapped. A line was then drawn on the map bisecting the distance between the outermost tree of the clone and its nearest outside neighbour. This line gave the clonal boundaries. The clonal maps are in Appendix I.

Clonal boundary delineation is difficult. Steneker (1973) drew in clonal boundaries by joining together ramets at the edge of the clone. The problem with this method is that even in a stand with a closed canopy, the area made up of all the clones will always total something less than 100 percent of the area of the stand. An alternative would be to draw in the boundaries adjoining the outermost points to which the root system extends. This presents obvious logistical problems. Since there is certainly some root overlap between trees, this method would yield a total area greater than 100 percent. A third alternative would be to

locate the boundary based on crown extension. This is a reasonable compromise between the first two methods; however, gaps would still occur, and the total stand area of all the clones would still be less than 100 percent. The method followed in this study is intended to be a compromise among the three methods mentioned above. With this method, total stand area will always be 100 percent. Obviously, adjustments in this technique would need to be made if large openings in the stand existed. Also, areas dominated by other species or landforms which prevent the site from being occupied by aspen would be eliminated.

The area of each clone was determined by using a planimeter on the field maps and multiplying by the appropriate scale. Stocking figures were determined by dividing the number of stems in the clone by the clonal area in hectares.

In both study areas, five trees were randomly selected from each of the six clones for further measurements. This was done by numbering each tree within the clones and using a random numbers table. The sample trees were randomly chosen to eliminate human bias in the sample selection. This method also assumed the five trees to be representative of the clone as a whole.

Each of the selected trees was destructively sampled for biomass determinations of the bole. Biomass is defined as oven-dry weight. Biomass was used for several reasons. Promnitz and Wray (N.D.) felt that an increasing emphasis

will be placed on dry-mass production in the future. Bartos and Johnston (1978) also emphasized the great need for biomass data on aspen. In addition, biomass is a useful measure for inter-specific comparisons. For example, Kramer and Kozlowski (1960) noted that wood of high density would produce twice as much pulp of the same volume of low density wood. They also pointed out that the specific gravity of wood generally increased with age. This may be important in this study, because there is some age variation within and between the two study sites. Biomass measurement circumvents the problem of varying specific gravities and allows examination of productivity strictly in terms of useable material. Oven-dry weight is used instead of green weight to avoid problems of varying water content. Water content can vary from 130 percent of dry weight in winter to 65 percent in summer, with significant diurnal fluctuations (Bendsten and Rees 1962). Use of dry-weight productivity eliminates problems of sampling time and comparisons with other work.

Ovington (1962) emphasized that a distinction should be made between plant matter of economic value and total primary production. At present, the bole is the most highly utilized portion of the tree. There are several reasons for this. First, the majority of the biomass of the tree is located in the bole. Bartos and Johnston (1978) found that the bole contained from 48 to 60 percent of the total above ground biomass. Second, the percentage of bark increases with height into the crown, ranging from 12 percent on the

lower bole to over 50 percent in the crown (Zavitkovski 1971, I.U.F.R.O. 1971). Bark is largely undesirable and can be considered as cull (IUFRO 1971). Third, harvesting the entire above-ground portion of the tree removes up to three times more nutrients from the site than harvesting only the bole (Alban, Perala, and Schlaegel 1978). Finally, difficulty in harvesting and high transportation costs further discourage utilization of the crown. In this study the merchantable bole was considered to be the segment of the tree from a 0.2 meter high stump to where the stem tapered to 7 centimeters in diameter or where branching determined the limits of merchantibility.

The same general procedures outlined in I.U.F.R.O. (1971) and Bartos and Johnston (1978) for determining bole biomass were used. Each sample tree was felled leaving a 0.2 meter stump. Starting at the base, the bole was sectioned into one meter lengths and the green weight was measured. The green weight of a disc at the bottom of each section also was measured. The discs were air-dried for two weeks, oven-dried for one week at 70 C, and weighed. The following calculations were then carried out to determine the biomass of the bole for each tree:

Equation 1

$$\text{Bole Biomass} = \Sigma \left(\frac{\text{section green weight}}{\text{disc green weight}} \right) \times \text{disc oven-dry weight}$$

Throughout its range aspen is very susceptible to decay (Graham et al. 1963, Jones and Harper 1976, Anderson et al. 1977). Incidence of decay seems to vary considerably among clones (Graham et al. 1963, Jones and Harper 1976, Steneker 1972 and 1976). Hinds and Wengert (1977) and Anderson et al. (1977) discussed the occurrence and implications of both stain and decay. They concluded that although heart rot was a deductible defect, stain in the initial stages did not greatly reduce tissue strength and, therefore, was not a valid cull deduction. As this paper has been geared towards possible management practices and considers only the merchantable portion of the tree, it was felt that an accounting should be made of this type of cull. Therefore, after the oven-dry weights were measured, advanced decay was removed and each disc was reweighed. Stain and incipient decay were not removed. Advanced decay was considered to be anything which could be knocked out of the disc with the butt end of a screwdriver. The difference between the two oven-dry weights was the unuseable biomass or rot. The total decay in the bole was calculated in a similar fashion to biomass:

Equation 2

$$\text{Loss in bole due to decay} = \sum \left(\frac{\text{section green weight}}{\text{disc green weight}} \right) \times \text{disc oven-dry weight}$$

This technique makes the assumption that the proportion of rot loss in each disc is representative of the rot loss

which occurs in the entire section. The loss in bole biomass due to decay was subtracted from the initial biomass determination for each tree to yield the net or sound biomass in the bole. This is the measure of productivity used in all subsequent calculations and discussions.

Statistical Methods:

A number of analytical methods were used to test the hypotheses and objectives (Table 2).

Table 2. Table of statistical analyses performed on each hypothesis and objective.

Objectives and Hypotheses	Manner in which presented	Confidence level
objective 1(clone areas)	graphical	---
hypothesis 1(biomass per tree within sites)	ANOCOVA,graphical	95%
hypothesis 2(biomass per tree between sites)	ANOCOVA,graphical	95%
objective 2(stocking)	graphical	---
hypothesis 3(biomass per hectare within sites)	ANOCOVA,graphical	95%
hypothesis 4(biomass per hectare between sites)	ANOCOVA,graphical	95%
objective 3(degree of genetic control)	heritability estimates	---

The aim of the first objective was to make a comparison of clonal areas within and between the two study sites. Since each clone has only one area value, no statistical test can be applied to examine the significance of differences among clones. Instead the area of each clone

will be graphically illustrated and will serve as a basis for discussion and interpretations. Clone maps (Appendix I) can also be examined to determine the comparative sizes and shapes of the clones.

The calculations for hypotheses 1 and 2 were done twice, once for each of the two study sites. An analysis of covariance was calculated using biomass per tree, adjusted for, age for each of the sample trees. The resulting F-test, with 95 percent confidence intervals, determined whether there were significant differences in tree biomass among clones on a shared site.

An analysis of covariance is a combination of standard regression analysis and analysis of variance. It is a regression on both categorical and numerical variables. In this case the different clones are the categorical variables, biomass per tree the numerical variable, and tree age the cofactor. The age cofactor acts to reduce the residual error by adjusting the biomass values so that the weight of each tree is based on a common age. This reduces biases in the results due to age differences among trees.

To test hypothesis 2 another analysis of covariance was performed, again, using the 95 percent probability level. The same thirty sample trees and basic raw data from each stand were used. Here, any differences due to clonal effects were ignored. Instead, the sample trees were grouped by site, and only one test performed between the two sites.

To further aid in the discussion and interpretation of

the first two hypotheses a graphical presentation of average biomass per tree for the clones on both sites was made. This figure presents the data after each of the biomass values has been adjusted so that all trees have a common base age of 85 years. Eighty-five years is an arbitrary benchmark, chosen so that it would fall midway between the average ages of the two sites.

In examining clonal stocking levels in objective 2 the same problem exists in trying to look for significant differences as in objective 1. Stocking levels, therefore, will be analyzed and presented in the same graphical manner as clonal areas.

Hypotheses 3 and 4 incorporate the clonal stocking levels with the biomass per tree data to see whether it enhances or lessens productivity differences among clones. Biomass for each tree was multiplied by the stocking level of the clone from which it was sampled. The result is that each clone has five values of biomass per hectare representing it. The same procedure, rationale, and statistical tests were followed as for hypotheses 1 and 2. Using 95 percent confidence levels an analysis of covariance was performed for each site to test the effect of clone on productivity. Next, the clonal effect was ignored and an analysis of covariance was performed between the two sites. The same type of graphical presentation is given for biomass per hectare as was given for biomass per tree.

The method most commonly used to examine the relative

importance of environmental variation and genetic variation on the phenotype of a plant is to calculate a broad sense heritability estimate (Wright 1976). This is an estimate of the degree of genetic control of a given trait and is expressed by the ratio between genetic variance and total phenotypic variance.

Equation 3

$$\text{broad sense heritability} = \frac{\text{genetic variance}}{\text{total phentotypic variance}} = \frac{\sigma^2_{Ac}}{\sigma^2_{Ac} + \sigma^2_{w}}$$

Genetic variance is the variance occurring among the clones in each stand and can be given as:

$$\sigma^2_{Ac} = [\,(SS_{Ac}/df_1) - (SS_w/df_2)\,]/r.$$

where:
- SS_{Ac} = sum of squares among clones
- df_1 = number of clones - 1
- SS_w = sum of squares of individuals within clones
- df_2 = number of clones (number of ramets - 1)
- r = number of observations / clone

Total phenotypic variance is the sum of the genetic variance plus the variance or error term among the individuals within the clones (σ^2_w), where $\sigma^2_w = SS_w/df_2$. The total phenotypic variance is therefore given as $(\sigma^2_{Ac} + \sigma^2_w)$. In all cases, heritability were calculated from variance components adjusted for age differences by covariance analysis. Due to the nature of heritability estimates no tests for significance were conducted. It is the relative strength of genetic control (low:0-30%, medium:30-60%, high: 60-100%) which should be considered rather than specific heritability

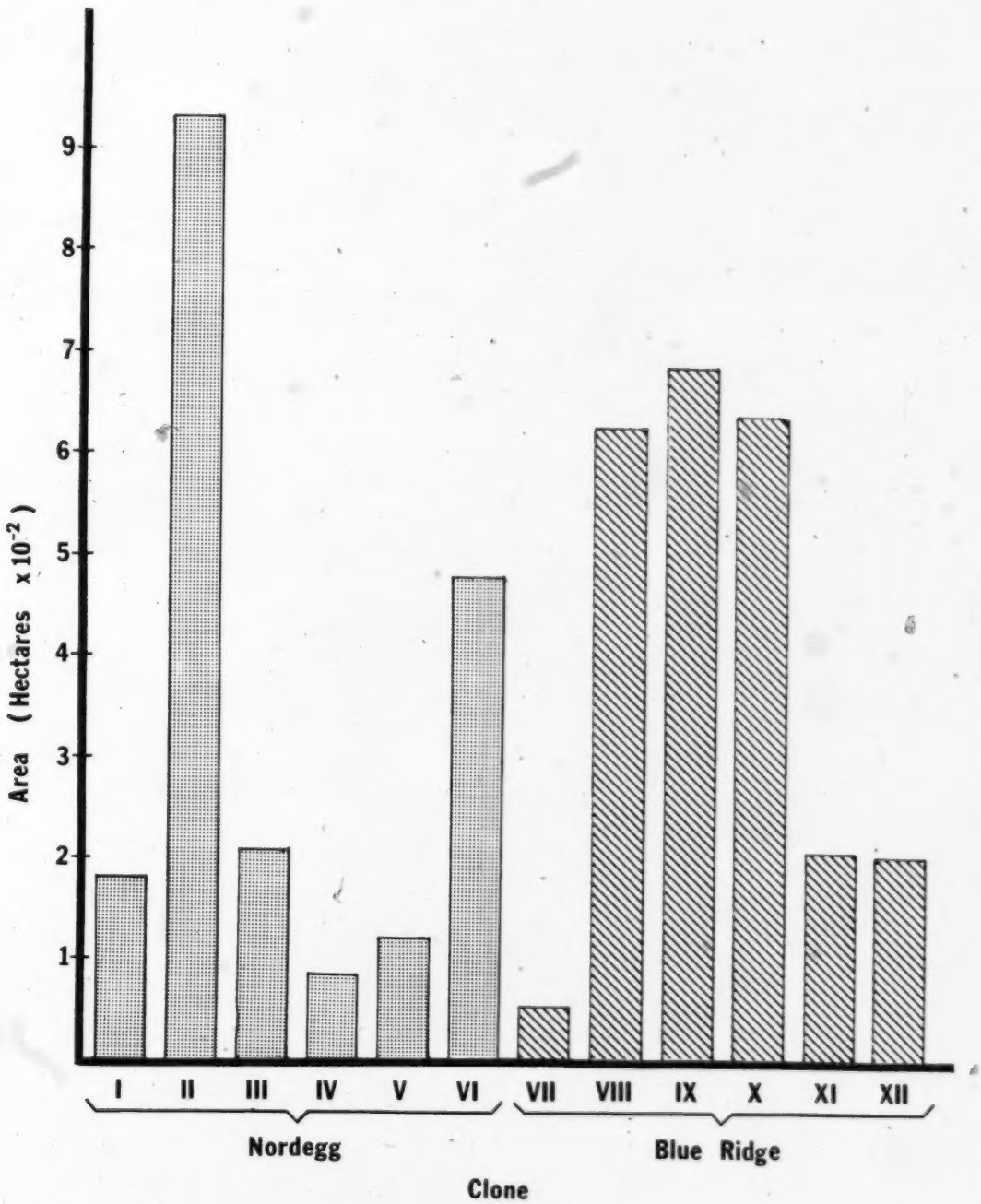
estimates (Dancik 1976). For any given trait heritability can change with the environment of the test site and the plants used in the test. Objective 3 was examined using heritability estimates of biomass per tree for the trees and clones on each site.

IV. RESULTS AND DISCUSSION

Area (Objective 1):

Figure 4 shows a comparison of clonal areas within and between the two study sites. In Nordegg the size of clones ranged from 0.010 to 0.095 ha with a mean of 0.035 ha. In Blue Ridge the range was from 0.005 to 0.070 ha with an average of 0.040 ha. The size differential between the largest and smallest clones at both sites is about 10 fold. There does not appear to be any appreciable difference in the average clone size between the two areas. Since the two study areas are quite different in environmental conditions and both show the same average and range in clone size, it appears that site conditions and clone size are unrelated. This conclusion, however, is based on only two sites with a sample size of six for each site. The small sample size and lack of a control or replication limits the confidence that one can place on the conclusion. One should remember that the same procedures for locating clonal boundaries are not used in all studies. Also, the two sets of clones used in this study are completely different from those used in other studies. However, Steneker (1973) also found a great fluctuation in size of clones in Manitoba. He noted a range from a single stem to 0.5 ha with a mean of 0.08 ha. Kemperman and Barnes (1976) found a range from 0.006 to 0.08 ha. The most typical size they found was 0.04 ha. They did not, however, state whether this was modal or a mean.

Figure 4. A comparison of clonal sizes within and between the Nordegg and Blue Ridge study sites.



Neither Steneker (1973) nor Kemperman and Barnes (1976) found any correlation between clone size and site conditions. Both speculated that clone size was related more to stand history than site. Patterns of initial seeding, disturbance history, competition, and inherent suckering abilities of the individual clones may be some of the factors contributing to present clone size. Differences in stand history between study sites, therefore, may also be a factor to consider when examining or comparing results with those of other researchers.

Biomass per tree (Hypotheses 1 and 2):

The first two hypotheses deal with examining differences in biomass per tree among clones on a shared site and among trees on different sites. There were significant differences ($P \leq .05$) in the biomass per tree among equal-aged clones on a shared sites (Tables 3 and 4). There were significant differences ($P \leq .001$) in biomass per tree between equal-aged aspen stands grown under different site conditions (Table 5).

Figure 5 illustrates average biomass per tree for each clone on the two sites using a common base age of 85 years. It does not show intra-clonal variability. However, variability among clones and the relative differences in biomass per tree between each of the sites can be seen. The average biomass per tree for Nordegg was 46.3 kg, ranging from 16.8 to 76.2 kg/tree. For Blue Ridge the average was

Table 3. Analysis of covariance of Nordegg tree biomass data by clone (Hypothesis 1).

Source of variation	Sum of squares	Degrees of freedom	Mean square	computed f	Probability
Treatment el. regr.	10,763.3104	5	2,152.6621	3.2526	<.05
Regression	11,708.0087	1	11,708.0087	17.6902	<.001
Error	15,222.2306	23	661.8361		
"Total"	37,693.5497	29			

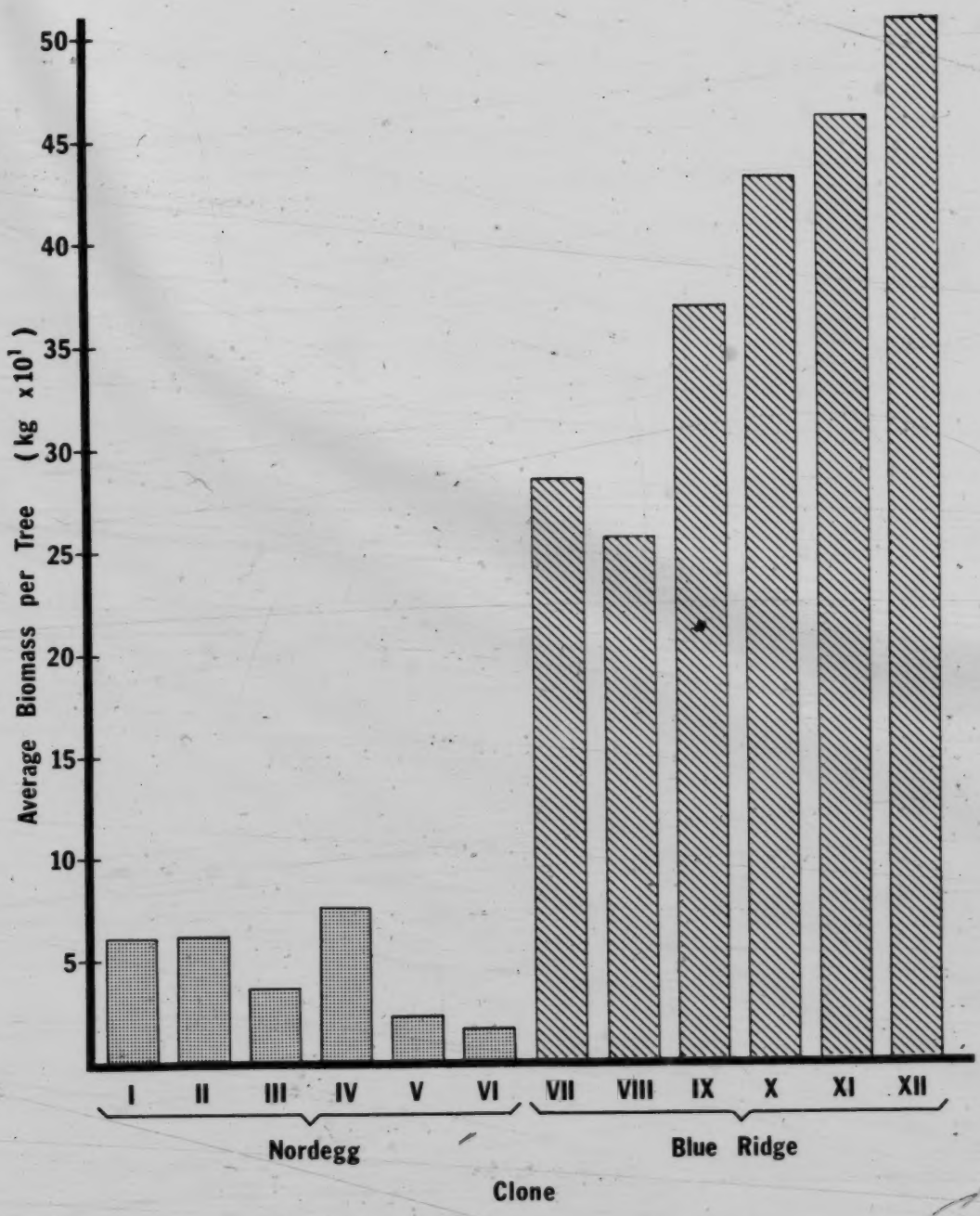
Table 4. Analysis of covariance of Blue Ridge tree biomass data by clone (Hypothesis 1).

Source of variation	Sum of squares	Degrees of freedom	Mean square	computed f	Probability
Treatment el. regr.	262,221.1400	5	52,444.2280	3.6419	<.05
Regression	211,055.5735	1	211,055.5735	14.6565	<.001
Error	331,203.5345	23	14,400.1537		
"Total"	804,480.2480	29			

Table 5. Analysis of covariance of tree biomass data between sites (Hypothesis 2).

Source of variation	Sum of squares	Degrees of freedom	Mean square	computed f	Probability
Treatment el. regr.	877,750.2074	1	877,750.2074	70.3760	<.001
Regression	93,818.8519	1	93,818.8519	7.5222	<.01
Error	710,920.7572	57	12,472.2940		
"Total"	1,682,489.8165	59			

Figure 5. A comparison of average biomass per tree for clones on two different sites using a common base age of 85 years.



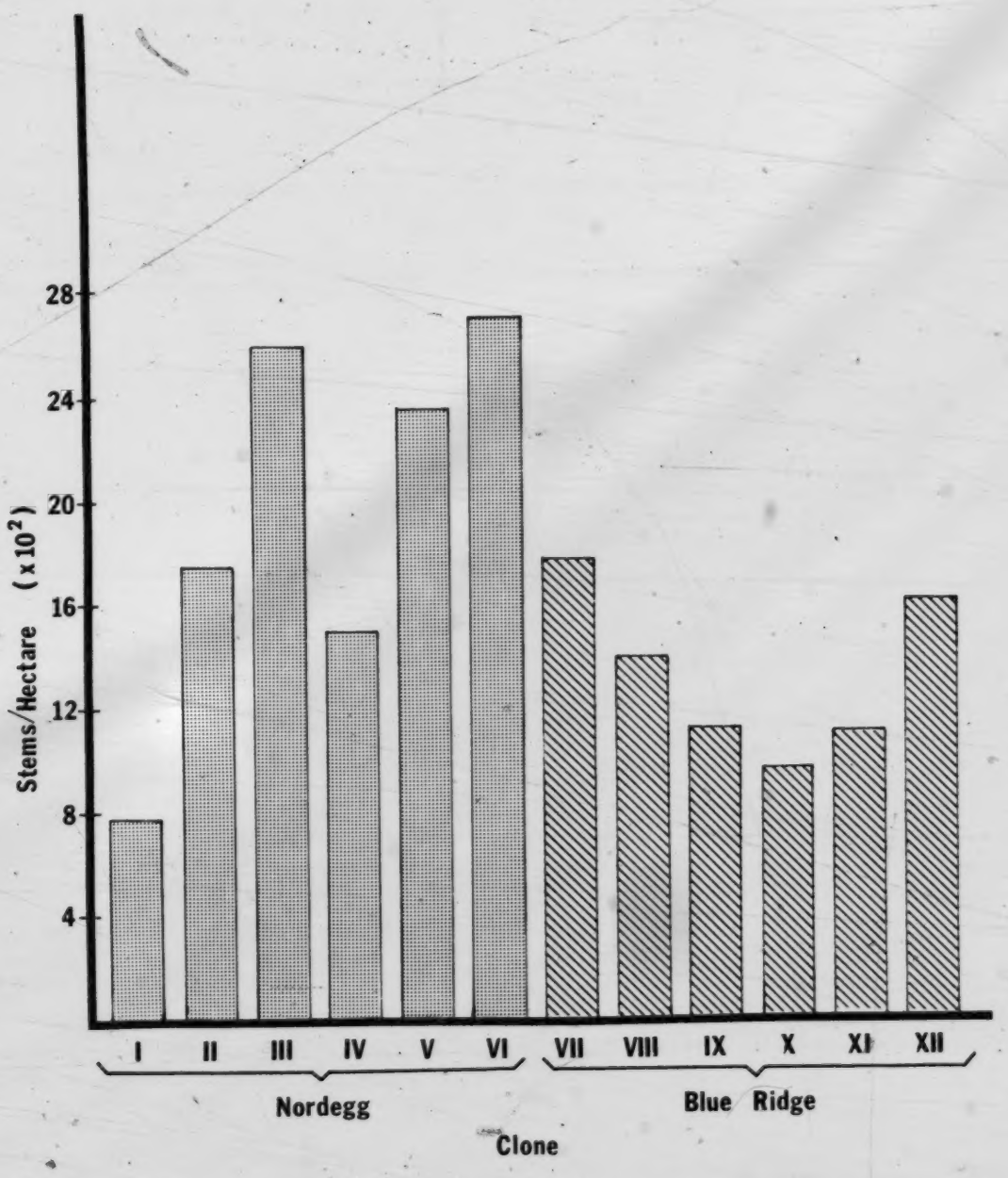
384.1 kg/tree with a range from 256.9 to 509.6 kg/tree. Average biomass at Blue Ridge was approximately 8 times greater than at the Nordegg site. In terms of the actual range, the Blue Ridge site also exhibits considerably more inter-clonal variation than Nordegg. If the relative variation among clones is examined for each site, Nordegg has almost twice the variability as Blue Ridge. However, absolute values are much more important in terms of usefulness or direct applicability towards aspen management.

Further discussion and interpretation of these results will be given after the stocking (Objective 2) and biomass per hectare (Hypotheses 3 and 4) results have been presented.

Stocking (Objective 2):

Figure 6 shows a comparison of clonal stocking levels within and between the two sites. There is considerable variation in stocking levels among clones. At Nordegg, stocking ranges from 773 to 2714 stems/ha with an average of 1944 stems/ha. In the Blue Ridge area the range is from 955 to 1766 stems/ha, averaging 1324 stems/ha. The harsher site, at Nordegg, has an average stocking level almost 50 percent greater than that at Blue Ridge. The range at Nordegg is almost twice that at Blue Ridge, as well. The explanation of this occurrence is multi-faceted and may not apply to all situations. Because of a combination of climatic, edaphic and other site factors, Nordegg has a drier and shorter

Figure 6. A comparison of clonal stocking levels within and between the Nordegg and Blue Ridge study sites.



growing season than Blue Ridge. Although close to the same age as the trees at Blue Ridge, the Nordegg stand appears to be stagnated at an earlier developmental stage. Earlier, it was shown that the average tree size was substantially less in Nordegg (Table 4); likewise the Nordegg site has a greater number of stems per hectare than the northern site. The Nordegg stand may not have undergone the same amount of natural thinning as stands on better sites, since the process of natural stand development could take longer on such a severe site. There are also a number of opposing factors which could effectively reduce stocking levels in particular areas. These could be a combination of both genetic and site factors. Some clones may not be as well adapted as others to reproduce and fully utilize all available growing space in a harsh environment. Rock outcrops and other natural barriers could also cause openings in the stand. Micro-habitat differences occur throughout any area and may also have an important influence on whether a tree can occupy the site.

Generally, the clones with the smallest stems also have the greatest stocking levels. This trend can be seen by examination of Figures 5 and 6. For example, clones III, V, and VI have the lowest average biomass per tree (Figure 5). These clones also have the three highest stocking levels (Figure 6). Barring any severely limiting factors, aspen, or any other plant, generally tends to fully occupy any available growing space. Since smaller trees take up less

space, more stems would be needed to make full use of the site. The relationship between tree size and stocking substantiates this. There are, however, individual cases which do not follow this trend. Clone XII, from Blue Ridge, has the largest average tree size and also one of the highest stocking levels for the site. Jones and Trujillio (1975a) also noted this phenomenon. Perhaps these clones are better suited to the conditions in which they grow. These clones are able to tolerate greater crowding without severely affecting the growth rate of the individual trees. Variations in micro-habitat may also contribute towards this variation. Whatever the reason, the trend shown by clone XII makes it a superior clone for useable biomass production and should be selected for further study.

Fralish (1972) reported typical stocking levels of 660 to 880 stems per hectare for mature (55 to 60 years old) aspen stands. He also pointed out that the time it takes for a stand to reach maturity varies with site. However, he did not report specific site information. Kirby, Bailey, and Gilmour (1957) also noted that the time it takes for an aspen stand to reach maturity is directly related to site conditions. The range of stand densities found by Fralish (1972) are less than half of those found in this study. His study site was located in Illinois, and it is likely that the habitat conditions on which he based his results were considerably different than those examined in this study. Since the growing season in Illinois generally would be

longer, it is likely that the average tree size would be larger, and it would require fewer trees per hectare to fully occupy and utilize the site.

In this study stocking varies substantially among clones and among stands growing under different site conditions. Also, the term "mature" is arbitrary and may vary according to the worker and context in which it is used. Reported stocking levels in natural stands, therefore, are often not compareable.

Biomass per hectare (Hypotheses 3 and 4):

Biomass per hectare among clones and between sites was also compared.

Baskerville (1965) stated that as stocking increased, overall levels of production increased to the point where full occupancy of the site was achieved. This would indicate that, in this case, once the stocking levels of each clone are combined with the biomass per tree data (biomass per hectare) the differences in productivity among clones should decrease.

There are significant differences ($P<.001$) in biomass per hectare among clones for Nordegg (Table 6). At Blue Ridge the differences are significant at the 99 percent level (Table 7). When the two sites are compared, differences are significant at the 99.9 percent level (Table 8). The biomass per hectare values at Nordegg range between 39,000 to 140,000 kg/ha with an average of 77,619 kg/ha. At

Table 6. Analysis of covariance of biomass per ha in each clone at the Nordegg site (Hypothesis 3).

Source of variation	Sum of squares	Degrees of freedom	Mean square	computed f	Probability
Treatment el. regr.	211,411,446,700.0	5	42,282,289,340.0	17.3636	<.001
Regression	295,059,118,840.0	1	295,059,118,840.0	121.1687	<.001
Error	56,007,553,970.0	23	2,435,111,042.0		
"Total"	106,654,610,523.6	29			

Table 7. Analysis of covariance of biomass per ha in each clone at the Blue Ridge site (Hypothesis 3).

Source of variation	Sum of squares	Degrees of freedom	Mean square	computed f	Probability
Treatment el. regr.	593,249,179,200.0	5	118,649,835,800.0	4.5645	<.01
Regression	311,291,237,604.0	1	311,291,237,604.0	11.9755	<.001
Error	597,862,491,800.0	23	25,994,021,380.0		
"Total"	1,502,402,908,604.2	29			

Table 8. Analysis of covariance of biomass per ha between the Nordegg and Blue Ridge sites (Hypothesis 4).

Source of variation	Sum of squares	Degrees of freedom	Mean square	computed f	Probability
Treatment el. regr.	1,282,423,093,000.0	1	1,282,423,093,000.0	52.7432	<.001
Regression	106,098,495,081.0	1	106,098,495,081.0	43.6359	<.001
Error	1,385,925,372,000.0	57	24,314,480,210.0		
"Total"	2,774,446,960,080.6	59			

Blue Ridge the range is from 366,000 to 810,000 kg/ha, averaging 510,807 kg/ha.

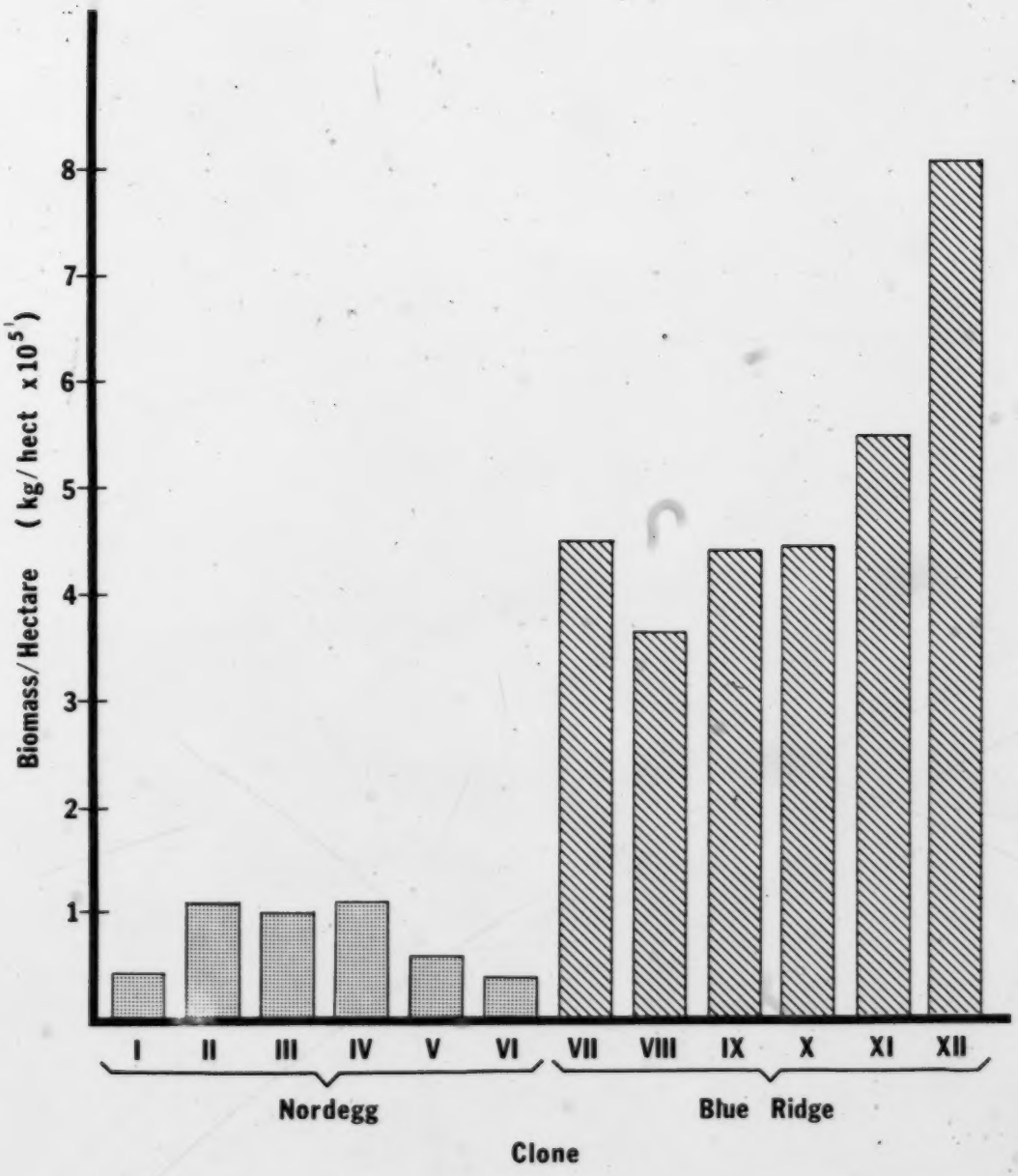
These figures, together with Figure 7, show the interclonal variation in biomass per hectare for each of the two sites, using a common base age of 85 years. The range and variation between sites is also shown.

Peterson et al. (1970) found an average bole biomass of 77,110 kg/ha, in a 66 to 89 year old aspen stand on a poor site in southern Alberta. A 55 year old clone on a better site was found to have a biomass of 290,000 kg/ha. Although younger than the clones on the better site in this study (~25 years), the extrapolated productivity levels seem fairly consistent with those reported here. There can be no direct comparison of the actual site conditions, and the delineation of good, medium, and poor sites is somewhat arbitrary.

The average biomass per hectare for Blue Ridge is approximately 6.5 times greater than the Nordegg average (Table 9). When the biomass per tree averages were compared, the difference between Nordegg and Blue Ridge was about 8 fold. The results of this study concur with the figures postulated by Peterson et al. (1970). Despite this trend, the biomass per hectare differences between the two sites is still significant ($P<.001$). Also, the trend at the Blue Ridge site, having a greater absolute range in values among clones, still persists.

The trends noted here are consistent with the

Figure 7. A comparison of biomass per hectare for clones on two different sites using a common base age of 85 years.



observations of others. Zahner and Crawford (1965) noted considerable variation in height among clones on the same site. A United States Forest Service study (USDA 1977) claimed that, on the same site, variation in yield among clones could differ as much as 200 percent. In this study the yield in biomass per hectare among clones varied from 200 to 300 percent (Figure 7). Greene (1971) noted that inter-clonal variation was greater than intra-clonal variation. This implies that on any given site much of the observed variation in productivity among trees is the result of genotype, as opposed to varying site conditions. Van Buijtenen et al. (1959) reported that differences in productivity due to clones was slight when compared to the overall productivity differences among sites. The results of this study support these findings. A 200 to 300 percent variation in biomass among clones is considered slight when compared to the overall influence of site on biomass production. In this study the variation in biomass per hectare between sites is 650 percent. However, this statement should be viewed with caution since little information on site parameters or degree of site differentiation is available.

Jones and Harper (1976) and Greene (1971) both commented that sites where environmental stresses are minimal would have clones exhibiting the greatest variability in productivity. Variation in productivity at the Blue Ridge site supports this statement. Jones and

Harper (1976) also commented that greater natural selection on extreme sites might be the cause of reduced variation. Poorly adapted genotypes could have been out-competed and eliminated. On better sites any clone, once established, may persist for a long time.

Heritability (Objective 3):

The last objective was to determine the extent of genetic versus environmental control over production of biomass. Copony and Barnes (1974) noted that phenotypic differences observed in trees on the same site are good indicators of genetic differences. In the case of a clonal species such as aspen it can generally be said that differences among trees in the same clone are due to environmental factors whereas differences among clones are due to a combination of site conditions and heredity (Van Buijtenen et al. 1959). The statistical analysis used to guage the influence of genotype and environment is broad sense heritability (Wright 1976). Heritability remains constant over time within any given sample population (Mohn and Randall 1971). The 10 year difference between ages of trees on the two sites should not influence the results. The clones used in this study were not selected strictly randomly. They were chosen because they could be readily delineated. The choice of clones, then, may influence the heritability and gain estimates.

The broad sense heritability estimate for biomass per

tree for Nordegg was 31 percent. For Blue Ridge it was 35 percent. This means that about one-third of the total phenotypic variance exhibited was due to genetic aspects. This would be classified as moderate heritability. As a comparison, Mohn and Randall (1971) found heritability estimates for aspen height and diameter to be 30 to 50 percent and 20 to 35 percent, respectively. Although height and diameter are independent traits they are closely related to biomass. Lehn (1978 unpublished data) found a correlation (r^2) of 0.981 between biomass of the bole and the product of diameter breast height (dbh) squared and height.

The moderate heritability estimates reflect relatively high variation within the clones. Kittredge (1938) noted that even in what seems to be a uniform environment, differences in habitat occur, sometimes within a distance of a few feet. These micro-differences in habitat probably play a major role in influencing biomass production. Van Buijtenen et al. (1959) also claimed that slight age differences and positioning of suckers on the initial parent root may have some effect on biomass production.

In each of the two sites investigated, there was a large amount of clonal variability in terms of useful biomass production. This variability makes it possible for clonal programs to realize a gain in productivity for future generations. The expected gain in bole biomass would be approximately one-third of the difference between the mean of all clones and the mean of the selected clones. In

Nordegg, if the best clone of the six were selected, this could mean a gain of 9.2 kilograms per stem. In Blue Ridge the gain could be as much as 43.9 kilograms per stem. The expected gains in biomass are approximately 5 times greater in the Blue Ridge area. Any intensive management practices with aspen should, therefore, be concentrated on the better quality sites (Weigle and Frothingham 1911).

Future Research Needs:

This study examined the biological aspects of productivity as affected by clone and site. In order for this information to be of more use to forest industry an economic analysis should also be performed. A cost-benefit analysis should be performed on the data presented here to determine if the differences in productivity among clones are significant from an economic point of view. This would have considerable influence upon whether aspen should be managed on a stand or clonal basis.

As the heritability estimates and significance levels between study areas have indicated, both macro- and micro-habitat changes can significantly affect productivity levels. This indicates the need for a more in-depth study of cause and effect relationships of environmental and habitat conditions on growth rates. This type of information could be of great use in developing silvicultural practices for site preparation after a disturbance.

Reciprocal plantings of superior clones should be

carried out on different sites. This would give an indication of the phenotypic plasticity of given genotypes and would indicate whether high productivity levels of certain clones are limited to one type of site.

In this study a good example of a reciprocal planting or common garden trial would be with clones VI and XII, the lowest clone for bole biomass production in Nordegg and the highest producing clone in Blue Ridge.

Clones, such as number XII, which exhibit the unusual and desireable trait of combining large average tree size with high stocking levels should also be given further study; specifically to see whether this is a trait which can be selected for.

Considerable variation has been noted among aspen clones in many traits. Asexual reproduction is no exception (Lehn 1978 unpublished data). Clones which may be superior in biomass production may be inferior in sucker production. Clones which have superior phenotypic traits at maturity in the field should be tested for desireable suckering and field establishment characteristics.

Finally, having selected those clones to use in future harvests, silvicultural practices need to be developed which would promote the reproduction and expansion of superior clones.

V. CONCLUSIONS

In terms of coppice reproduction, genetic variability, and fast growth, trembling aspen occupies a unique position in our forests. These factors need to be given serious consideration in developing aspen management practices.

This paper examined various traits of aspen which related to currently useable biomass production, and analyzed them in terms of probable management strategies. The stocking and size of aspen clones were examined. Inter- and intra-clonal variation in biomass production was studied on two different sites on an areal and individual tree basis. Finally, the relative effect of site and genetic control over production was examined.

Two different sets of clones were studied: one set on a good quality site (near Blue Ridge) and the other on a site considered to be of poor quality for aspen growth (near Nordegg).

Clonal sizes varied up to 10 fold in each of the sites examined. Clone size is probably related more to stand history than to environmental or site conditions. It is possible that many clones originated immediately after the last ice age, 12,000 years ago. The present day clone size is likely related to the type and frequency of site disturbances and the relative ability of some clones to expand their boundaries at the expense of other clones.

There were significant differences among clones in stem biomass in each of the two study areas, as well as a significant difference in the average biomass per tree between the two sites. Considerable variability was shown in the average biomass per tree among clones growing under seemingly uniform site conditions. The Blue Ridge site has greater variation in actual biomass. This may be due to less rigorous natural selection against poorly adapted clones on this relatively favourable growing site.

Stocking levels on each of the sites were variable. Tree size was smaller and stocking was denser at the Nordegg site. The stand structure at Nordegg appeared similar to a stand of considerably younger developmental stage at Blue Ridge. There also was a greater range in stocking levels on the poor site. The higher level is due to overall earlier developmental stage of the stand. The sparse stocking of some of the clones may be a result of the intolerance of the tree to crowding, high inhibition of suckering by competition or shade, or physical site factors which would inhibit the presence of a tree. Occasionally a clone with a large average tree size also had a high stocking level. Clones which exhibit this combination need to be examined to determine whether selection for these two traits is possible.

Biomass per hectare significantly differed among clones on both sites. The difference in average biomass per hectare between the two sites, while significant, was less than the

difference in tree biomass between the sites, because of the effect of stocking levels. The better site was 8 times more productive than the poor site in average stem biomass, but only 6.5 times more productive in overall biomass per hectare. With respect to biomass productivity each site showed considerable internal variation with the better site having the greatest variability.

A 6.5 fold increase in biomass per hectare on one site over another indicates that site selection is critical to aspen management. This, of course, is somewhat dependent on the desired management objectives. At Nordegg, aspen form and growth is so poor, it may not be of any value for biomass production. This is particularly true since neighbouring spruce and pine stands, growing under the same site conditions, appear to have much better growth and form. Here, aspen might be most useful only as a "nurse crop" for spruce regeneration.

Broad sense heritability estimates for bole biomass were moderate. Approximately one-third of the variation in biomass of trees growing on each site was due to clonal or genetic control. Much of the residual variance could be due to micro-habitat differences within the clone. Age and position of the suckers could also affect the variance and heritability estimates. Possible gains from selection among the clones measured at the Blue Ridge site could be as high as 43.9 kilograms per stem. The results of this study and those of Brinkman and Rowe (1975) indicate considerable

possible gains from clonal selection. Selection programs should be concentrated on medium and good sites where they will obtain the best results (Fralish and Loucks 1975).

Aspen exhibits a phenomenal amount of variability among clones in almost every aspect. It is therefore important that the clone be the basic sampling unit in any type of forest inventory or site productivity work. It should be considered in all decisions pertaining to aspen management (Steneker and Wall 1970).

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APPENDIX I

Clonal maps for each of the six clones in the Nordegg and Blue Ridge study areas

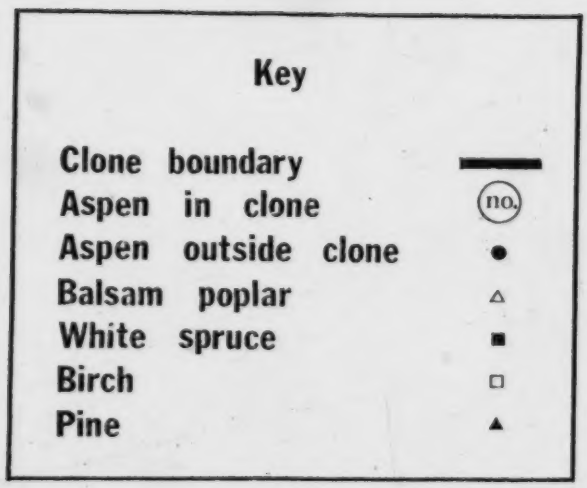
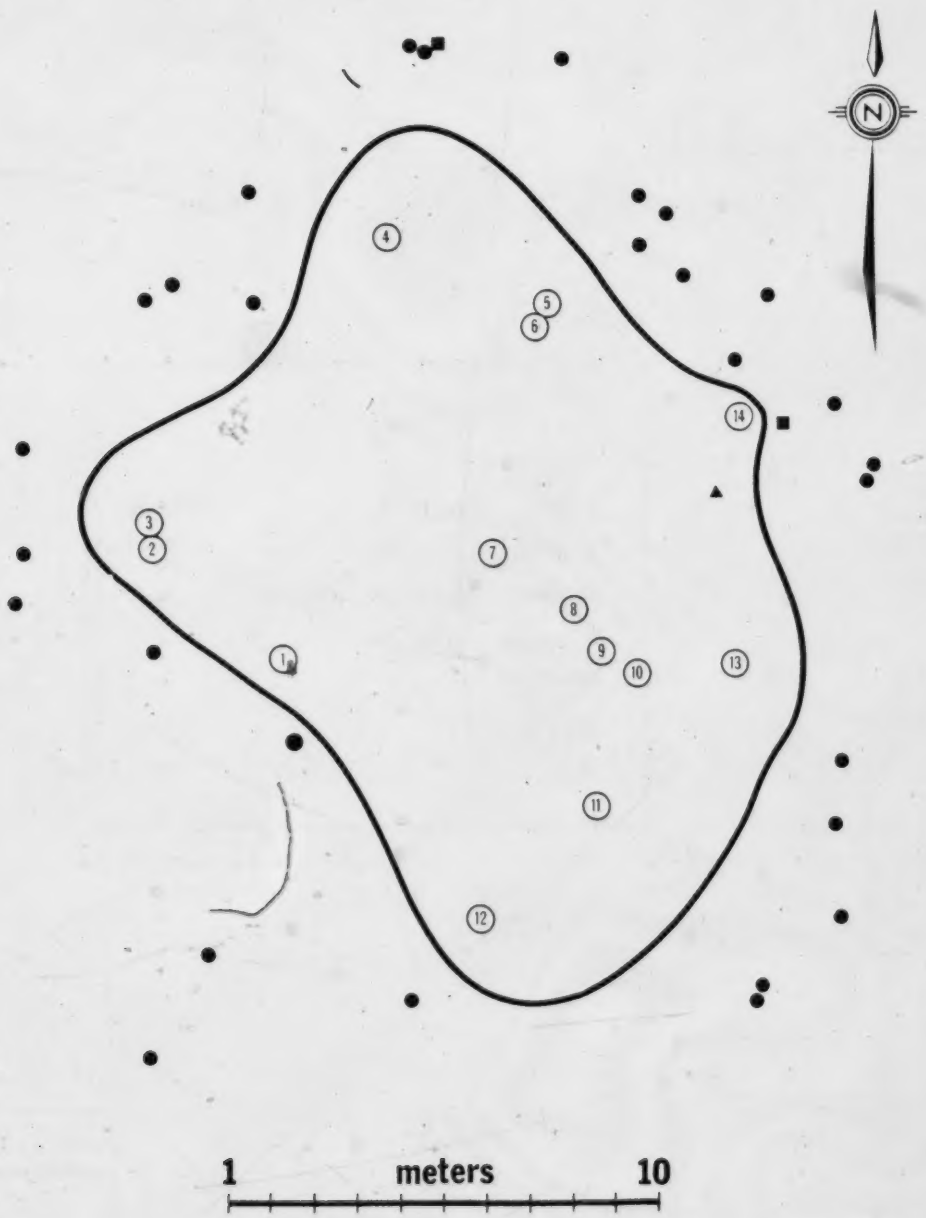

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 8. Nordegg - Clone I.



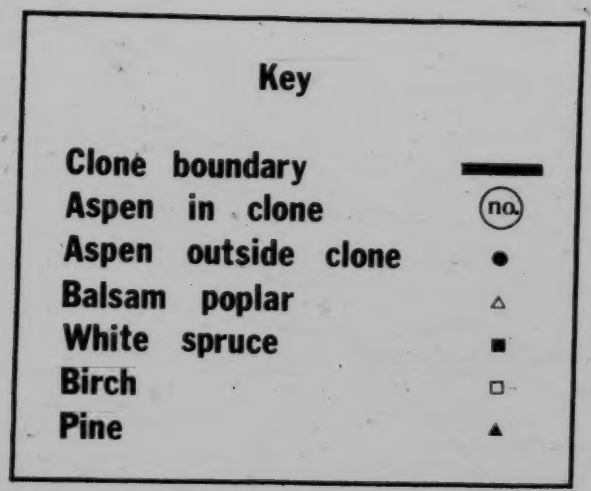
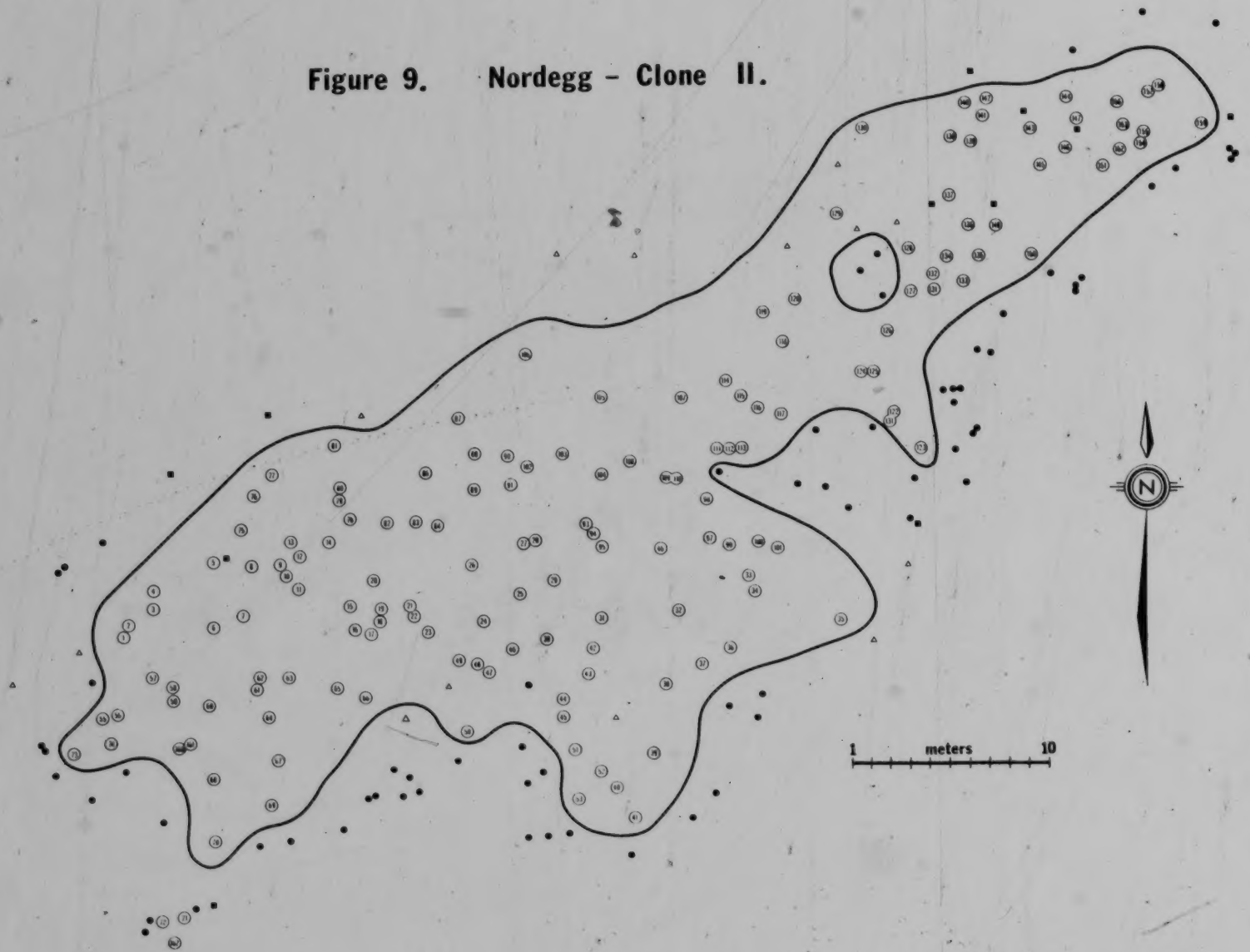

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 9. Nordegg – Clone II.



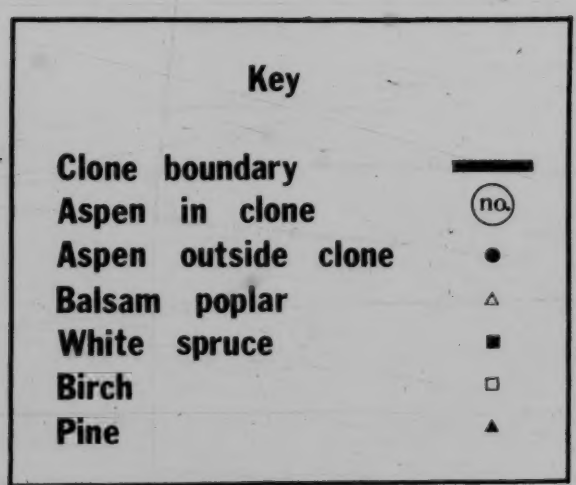
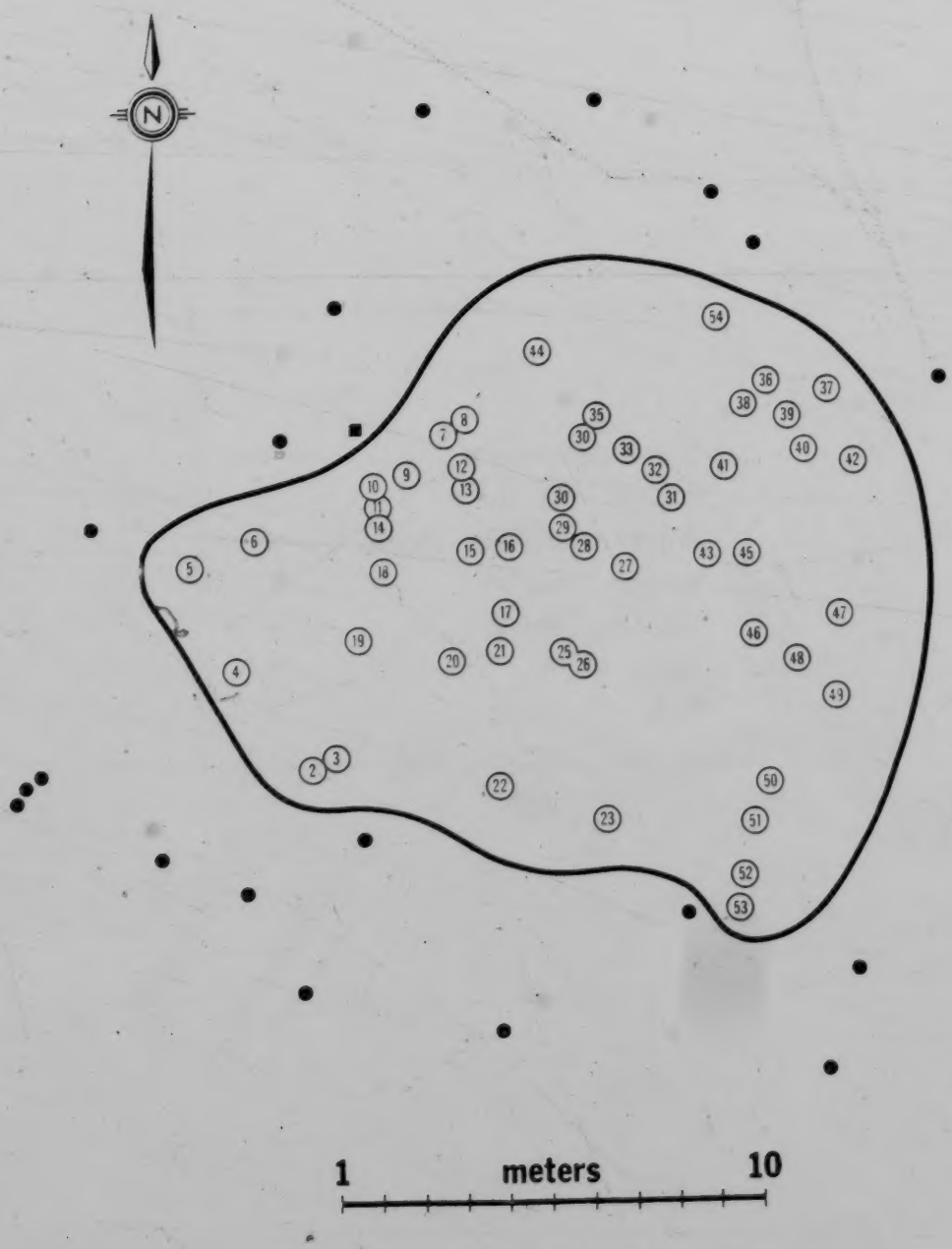

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 10. Nordegg - Clone III.



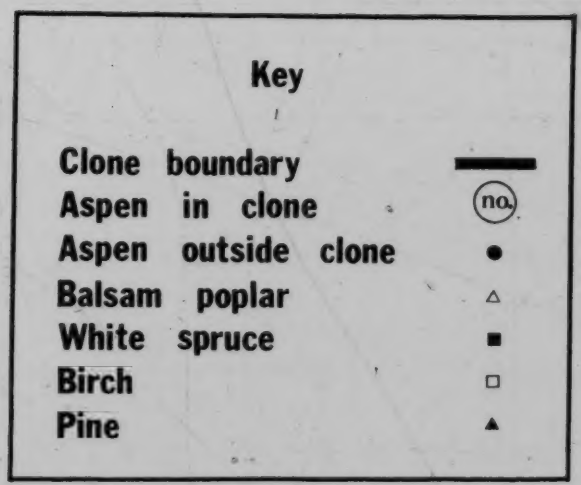
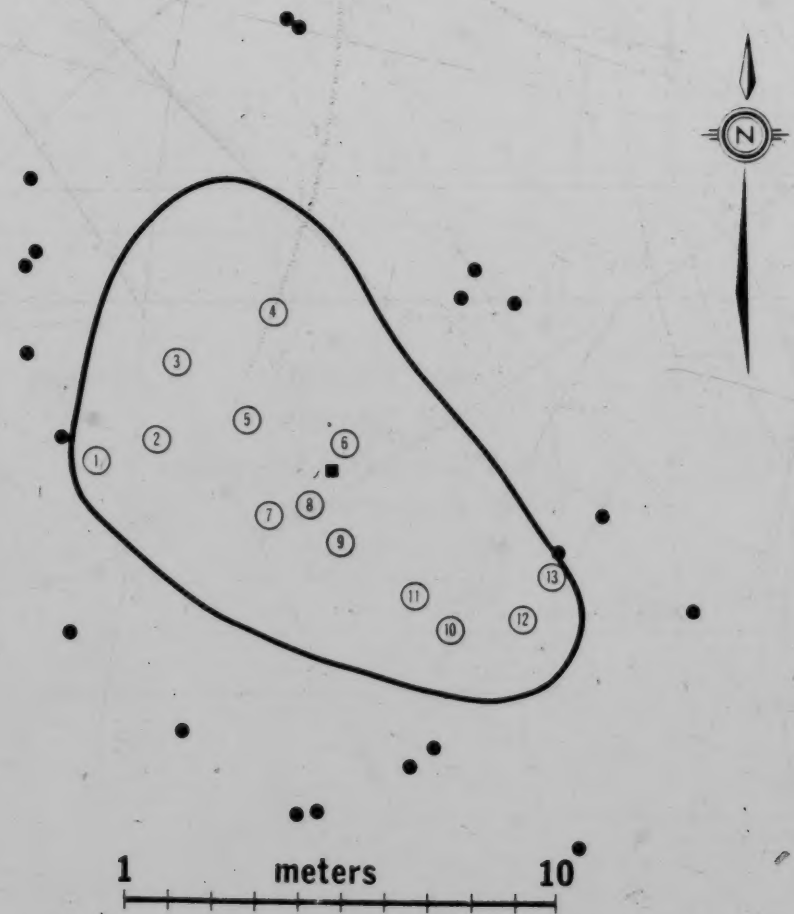

Key
Clone boundary
Aspen in clone
na
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 11. Nordegg - Clone IV.



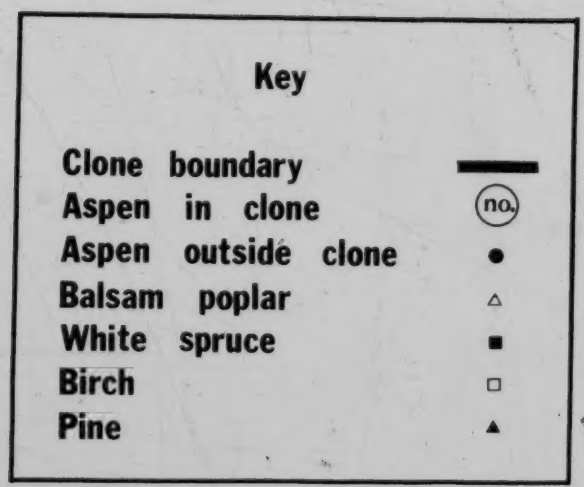
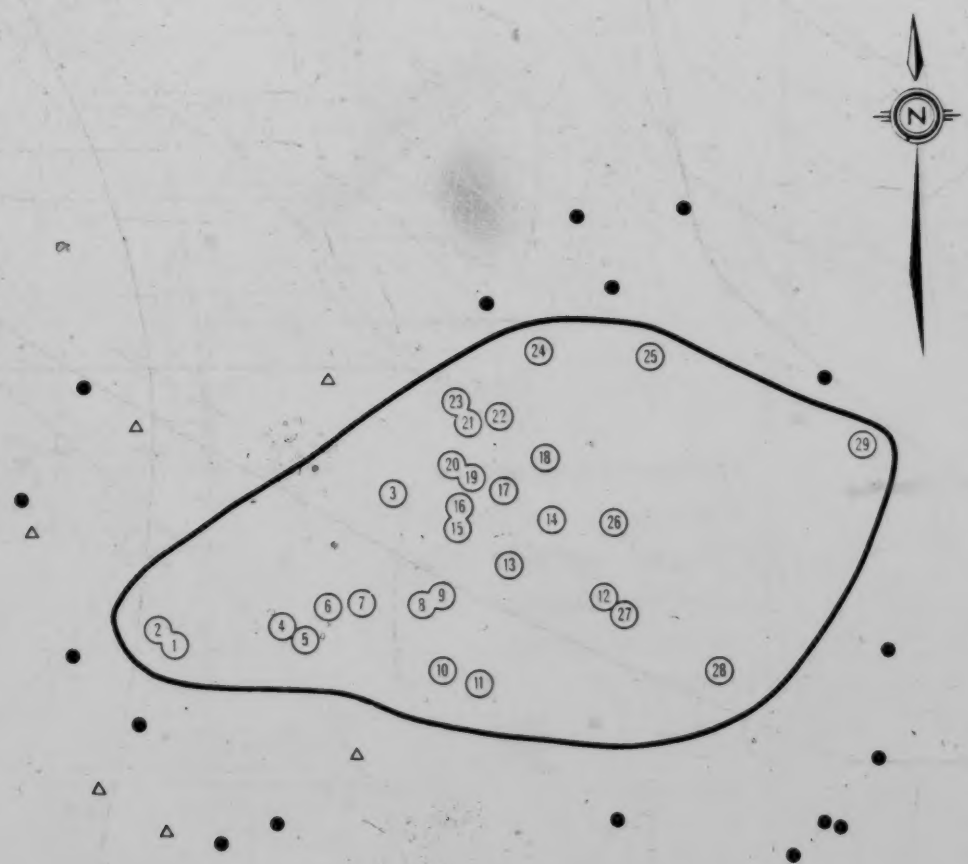

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 12. Nordegg – Clone V.



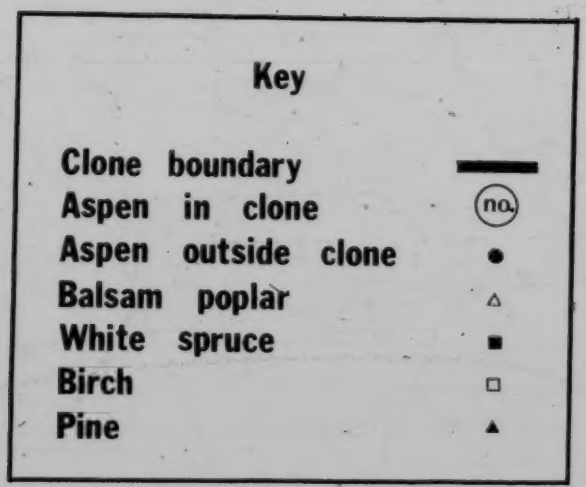
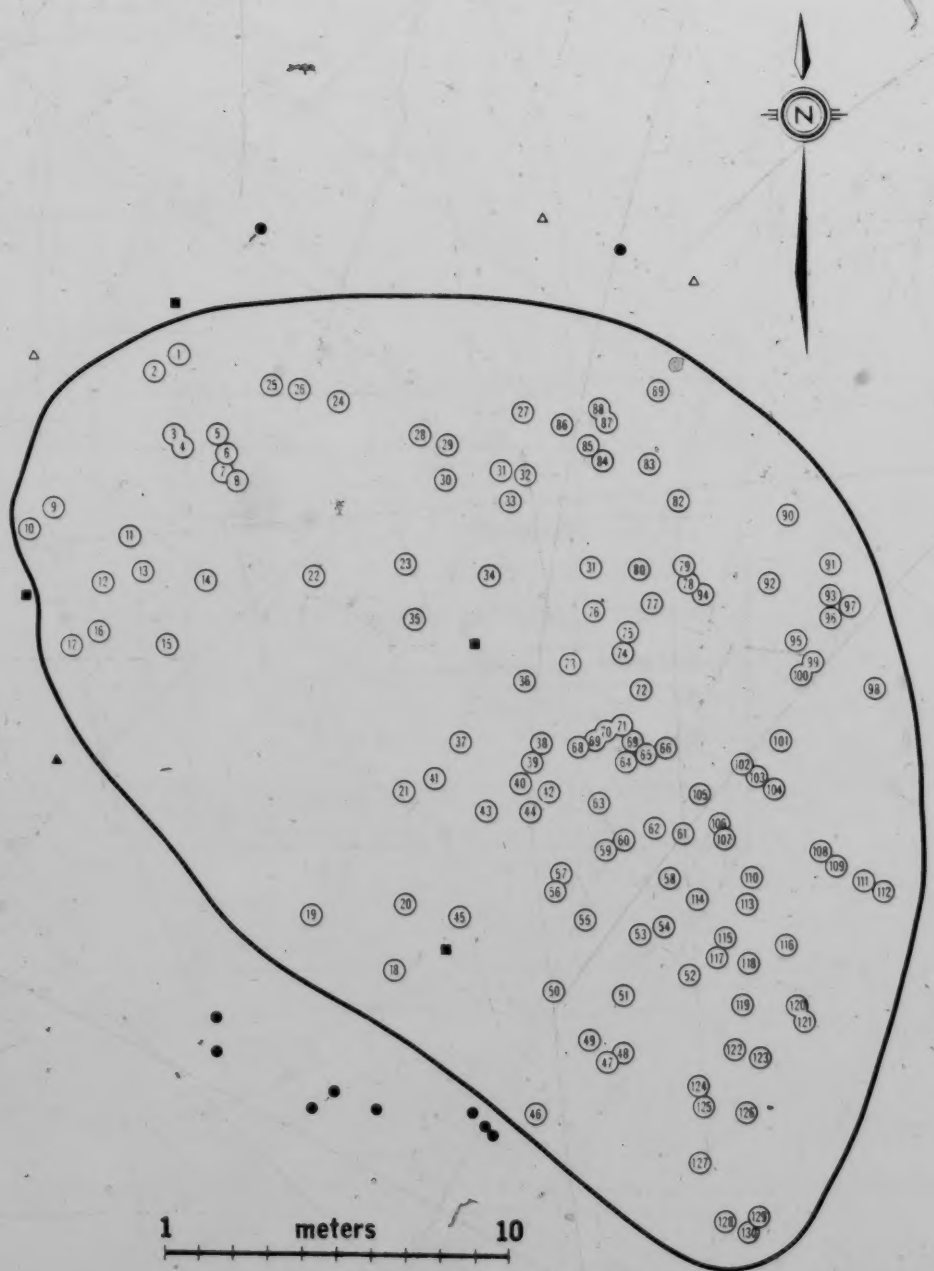

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 13. Nordegg - Clone VI.



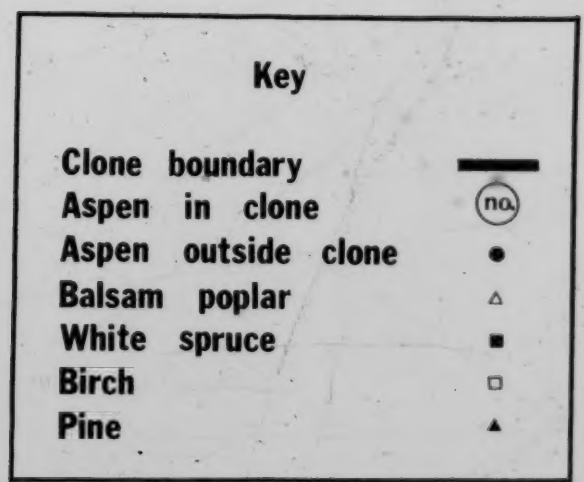
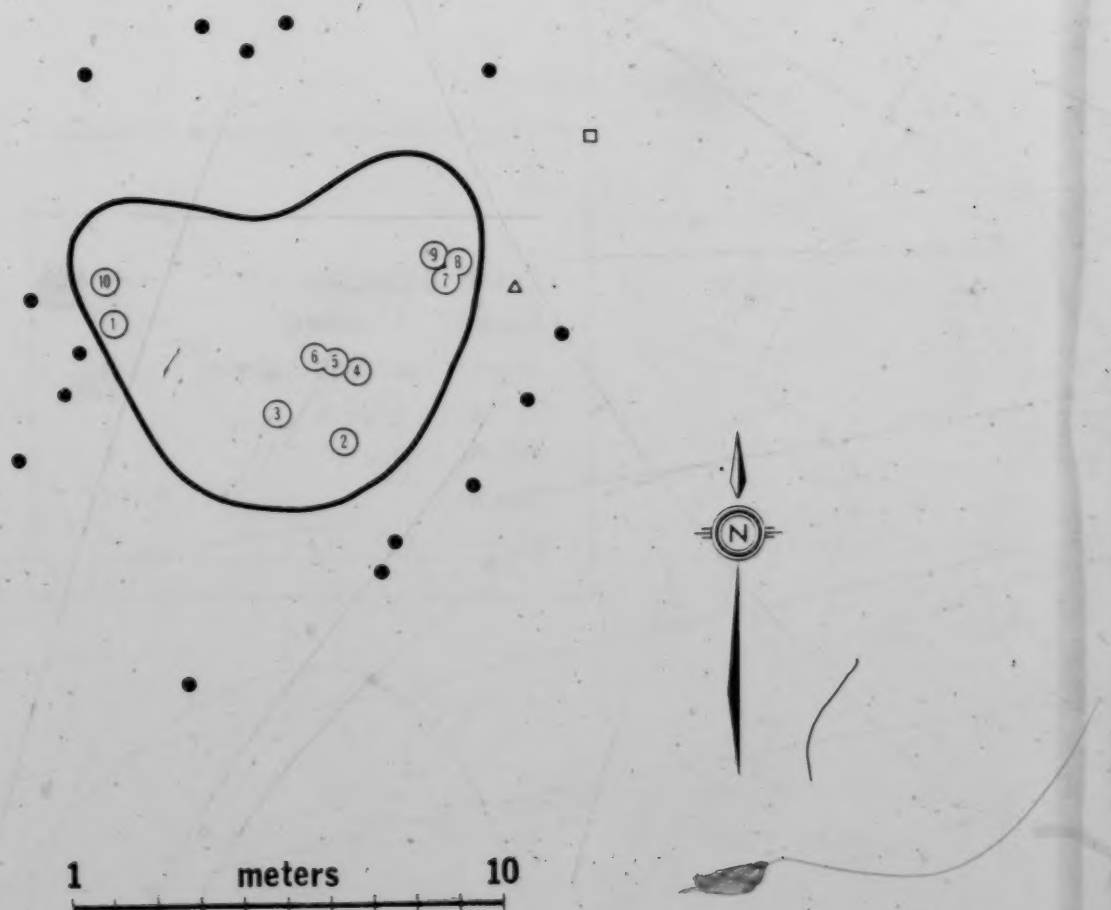

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 14. Blue Ridge - Clone VII.



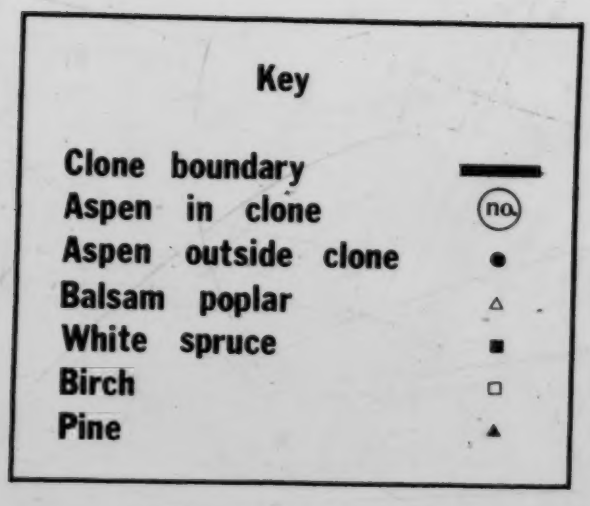
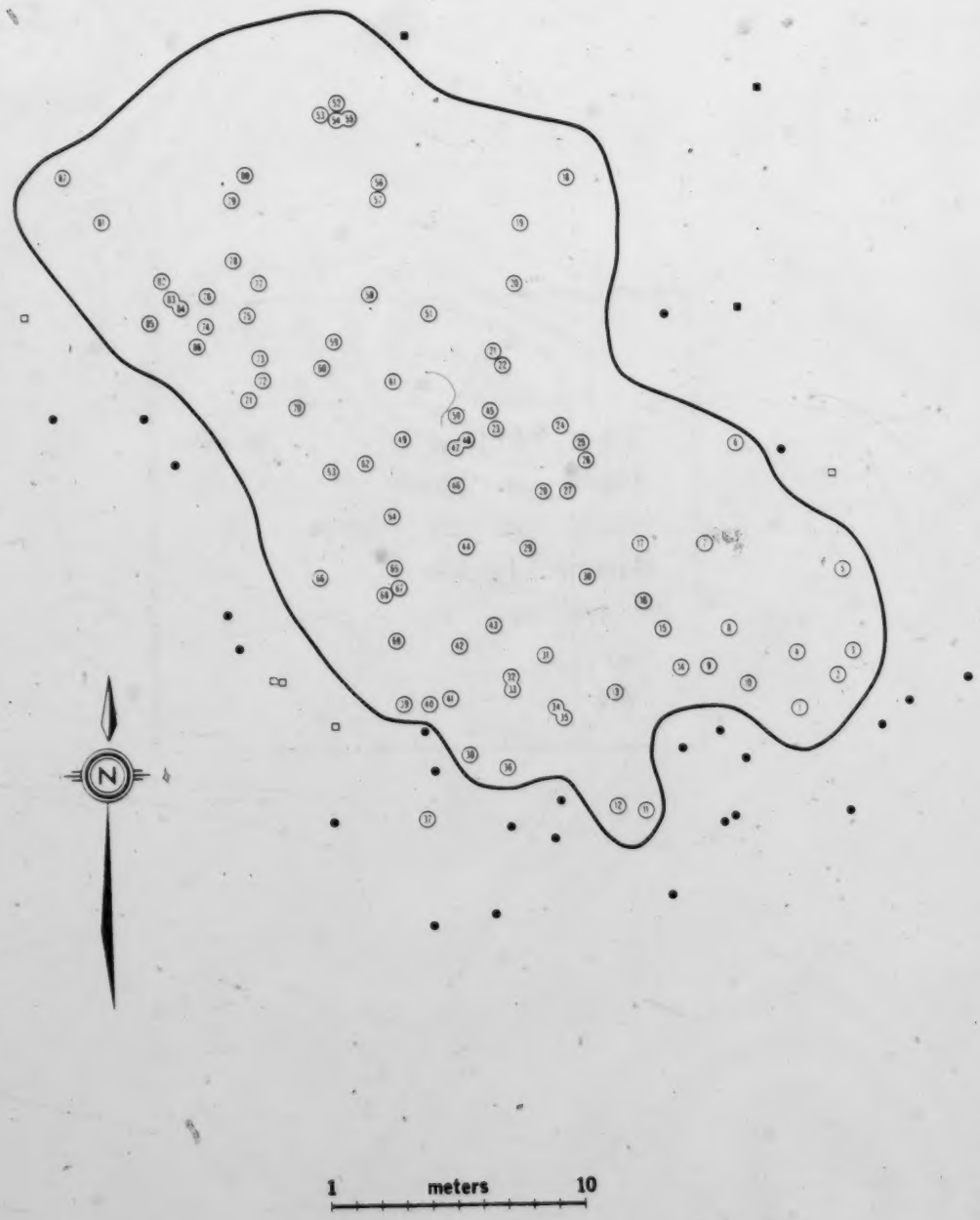

Key
Clone boundary
Aspen in clone
na
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 15. Blue Ridge - Clone VIII.



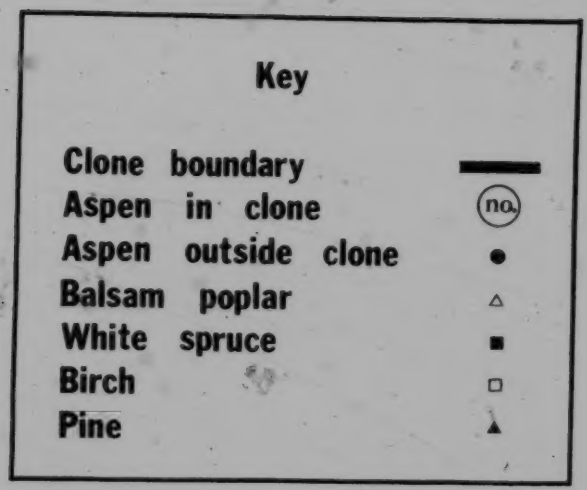

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 16. Blue Ridge - Clone IX.

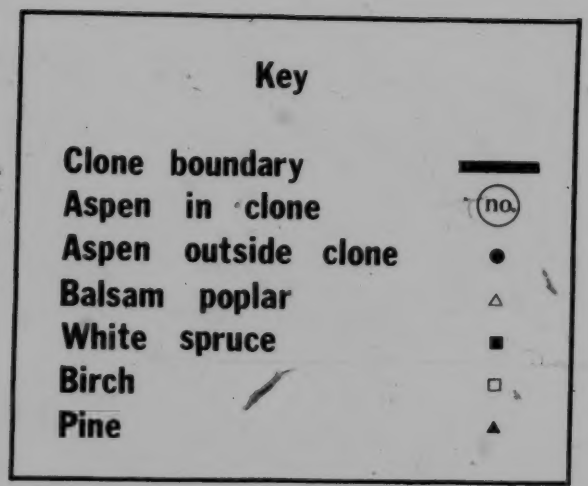

Key
Clone boundary
Aspen in clone
na
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 17. Blue Ridge - Clone X.

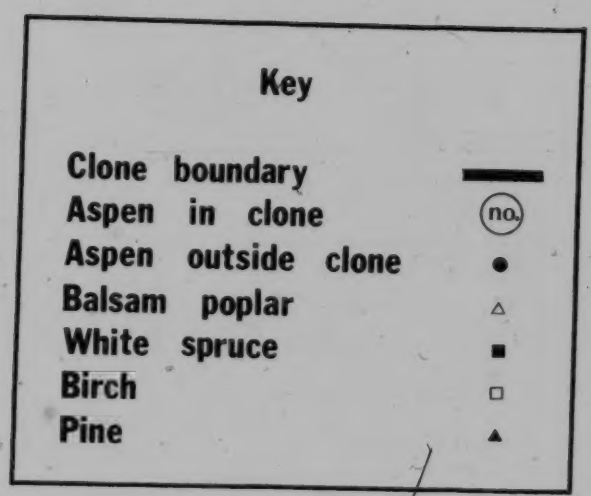

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 18. Blue Ridge - Clone XI.

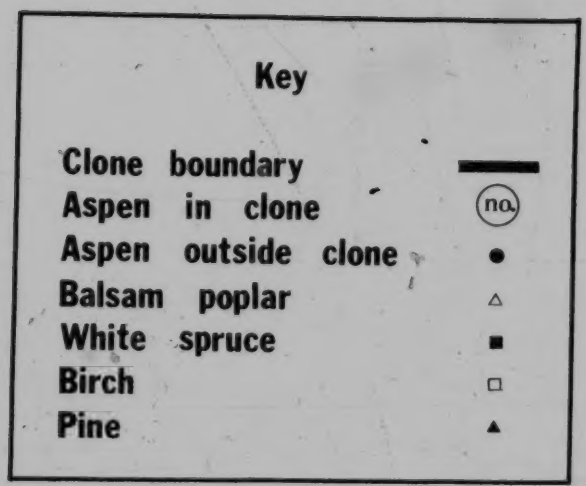
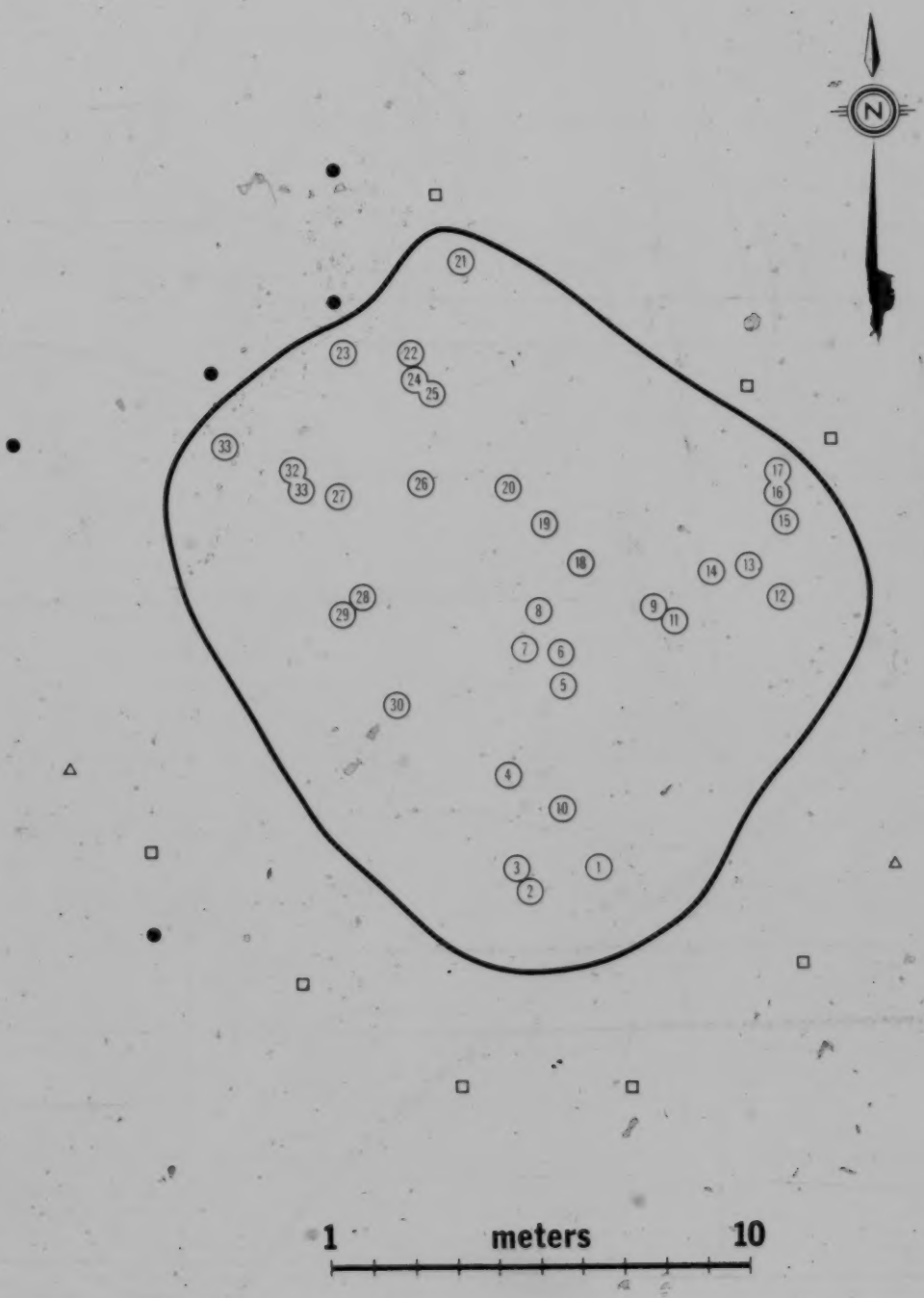

Key
Clone boundary
Aspen in clone
no.
Aspen outside clone
Balsam poplar
White spruce
Birch
Pine

Figure 19. Blue Ridge - Clone XII.



APPENDIX II

Basic field data and age adjusted biomass values for each of the six clones in the Nordegg and Blue Ridge study areas

Table 9. Basic field data for clones I and II in the Nordegg study area.

tree no.	dbh (cm)	tot. ht. (m)	age (yrs)	tot. bole bio.* (kg)	bole rot loss (kg)	bole sound wood (kg)	clone	area (ha)	no. of stems	stocking (stems/ha)	ave. bio. per tree (kg)	tot. bio. in clone (kg)	bio. per ha (kg)
5	13.0	16.1	91	49.6	1.1	48.5							
6	15.0	16.5	90	57.2	0	57.2							
4	16.1	15.7	86	77.8	0	77.8	I	.020	14	773	66.24	927.4	51235.4
10	14.7	15.4	86	61.6	0	61.6							
9	17.4	16.1	93	86.1	0	86.1							
160	15.5	16.2	96	66.8	0	66.8							
66	20.9	18.1	98	135.8	0	135.8							
76	18.0	17.3	108	90.7	0	90.7	II	.095	163	1738	80.98	13199.7	141628.1
100	16.2	16.2	106	71.8	0	71.8							
121	13.6	14.7	91	39.8	0	39.8							

* bio. = biomass

Table 10. Basic field data for clones III and IV in the Nordegg study area.

tree no.	dbh (cm)	tot. ht. (m)	age (yrs)	tot. bole *bio. (kg)	bole rot loss (kg)	bole sound wood (kg)	clone	area (ha)	no. of stems	stocking (stems/ha)	ave. bio. per tree (kg)	tot. bio. in clone (kg)	bio. per ha (kg)
11	10.3	10.9	89	15.5	0.7	14.8							
9	14.6	11.9	90	47.9	0.3	47.6							
13	14.7	12.2	91	50.4	0	50.4	III	.020	54	2589	41.28	2229.1	106861.0
45	16.7	13.8	85	75.9	0	75.9							
18	10.2	11.3	88	18.2	0.5	17.7							
13	12.6	11.0	86	26.6	0	26.6							
5	17.5	14.9	94	79.7	0	79.7							
3	21.3	15.6	89	128.5	0	128.5	IV	.010	13	1502	83.48	1085.2	125316.4
10	20.5	12.9	90	94.6	4.2	90.4							
9	20.8	13.9	89	92.1	0	92.1							

* bio. = biomass

Table 11. Basic field data for clones V and VI in the Nordegg study area.

tree no.	dbh (cm)	tot. ht. (m)	age (yrs)	* tot. bole bio. (kg)	bole rot loss (kg)	bole sound wood (kg)	clone	area (ha)	no. of stems	stocking (stems/ha)	ave. bio. per tree (kg)	tot. bio. in clone (kg)	bio. per ha (kg)
5	10.6	7.2	78	13.6	0	13.6							
16	16.0	12.2	96	55.6	0	55.6							
22	11.5	8.7	90	20.5	0	20.5	V	.010	29	2350	29.50	855.5	69327.4
23	11.4	9.7	95	19.2	0.6	18.6							
24	13.7	11.4	92	39.2	0	39.2							
105	6.6	8.2	83	1.4	0	1.4							
55	9.0	9.5	83	9.7	0	9.7							
60	8.1	8.2	77	7.4	0	7.4	VI	.050	130	2714	10.82	1406.6	29359.2
10	14.7	10.6	77	35.6	0	35.6							
51	6.4	6.9	80	0	0	0							

* bio. = biomass

Table 12. Basic field data for clones VII and VIII in the Blue Ridge study area.

tree no.	dbh (cm)	tot. ht. (m)	age (yrs)	tot. bole *bio. (kg)	bole rot loss (kg)	bole sound wood (kg)	clone	area (ha)	no. of stems	stocking (stems/ha)	ave. bio. per tree (kg)	tot. bio. in clone (kg)	bio. per ha (kg)
5	14.8	17.3	70	71.8	2.3	69.5							
8	19.9	20.8	82	176.8	0	176.8							
10	21.5	21.8	81	183.3	0	183.3	VII	.005	10	1766	134.8	1348.0	238162.5
3	19.1	19.9	71	128.3	0	128.3							
4	17.5	20.7	77	116.3	0	116.3							
30	16.8	19.3	78	88.3	0.1	88.2							
86	21.8	24.7	80	208.6	0	208.6							
73	20.4	24.1	81	192.4	0	192.4	VIII	.065	87	1388	187.0	16269.0	259473.7
14	16.1	21.2	82	100.3	0.3	100.0							
53	29.7	22.9	82	345.7	0	345.7							

* bio. = biomass

Table 13. Basic field data for clones IX and X in the Blue Ridge study area.

tree no.	dbh (cm)	tot. ht. (m)	age (yrs)	* tot. bole bio. (kg)	bole rot loss (kg)	bole sound wood (kg)	clone	area (ha)	no. of stems	stocking (stems/ha)	ave. bio. per tree (kg)	tot. bio. in clone (kg)	bio. per ha (kg)
39	24.0	24.6	81	173.2	11.4	161.8							
10	27.5	24.2	78	291.6	15.2	276.4							
9	27.0	26.2	79	326.4	0	326.4	IX	.070	77	1119	295.9	22784.3	331022.8
17a	32.6	24.5	82	452.5	0.5	452.0							
41	26.0	25.5	82	276.5	13.7	262.8							
52	33.9	27.8	82	567.8	0	567.8							
53	32.1	26.9	82	428.4	0	428.4							
26	20.5	23.3	80	187.0	0.1	186.9	X	.065	61	955	372.0	22692.0	355339.8
43	26.2	25.8	82	310.2	0.2	310.0							
22	27.7	24.4	80	366.7	0	366.7							

* bio. = biomass

Table 14. Basic filed data for clones XI and XII in the Blue Ridge study area.

tree no.	dbh (cm)	tot. ht. (m)	age (yrs)	* tot. bole bio. (kg)	bole rot loss (kg)	bole sound wood (kg)	clone	area (ha)	no. of stems	stock-ing (stems ha)	ave. bio. per tree (kg)	tot. bio. in clone (kg)	bio. per ha (kg)
18	28.5	25.9	80	378.7	0	378.7							
17	18.8	22.9	73	150.0	0	150.0							
19	36.1	21.9	82	529.6	0	529.6	XI	.020	23	1103	366.6	8431.8	404209.0
11	28.5	23.9	82	379.9	0	379.9							
6	29.3	23.3	78	394.6	0	394.6							
32	28.1	24.5	82	339.9	0	339.9							
22	22.9	21.2	82	218.6	0	218.6							
24	15.8	13.3	55	42.4	0	42.4	XII	.020	33	1614	376.1	12411.3	607206.4
5	36.5	25.7	82	682.3	0	682.3							
16	35.3	26.3	82	597.3	0	597.3							

* bio. = biomass

Table 15. Adjusted biomass per hectare and average biomass per tree values for each of six clones in the Nordegg and Blue Ridge study areas using a common base age of 85 years.

	Clone	Biomass per hectare ($kg\ ha^{-1}$)	Average biomass per tree ($kg\ tree^{-1}$)
Nordegg	I	42804.9	61.2
	II	111148.0	63.3
	III	99675.1	37.0
	IV	113788.8	76.2
	V	58926.7	23.3
	VI	39369.3	16.8
Blue Ridge	VII	450681.6	274.6
	VIII	365777.6	256.9
	IX	442197.6	369.0
	X	447025.7	432.4
	XI	549239.0	461.9
	XII	809918.0	509.6